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## Synalpheus shrimp from Carrie Bow Cay, Belize. Systematics, phylogenetics and biological observations (Crustacea: Decapoda: ; Alpheidae)

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*Synalpheus* SHRIMP FROM CARRIE BOW CAY, BELIZE.

SYSTEMATICS, PHYLOGENETICS AND BIOLOGICAL OBSERVATIONS

(CRUSTACEA: DECAPODA: ALPHEIDAE)



A Dissertation

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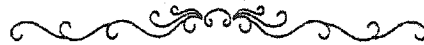
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In Partial Fulfillment

Of the requirements for the Degree of

Doctor of Philosophy



by

Rubén Ríos González

2003

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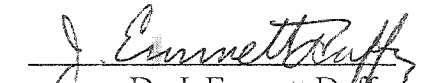
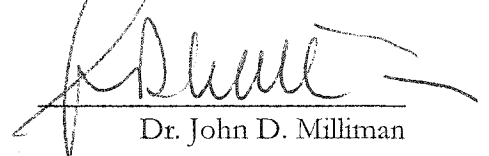
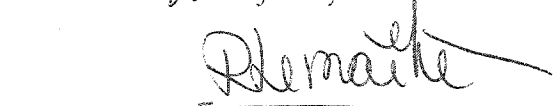
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## ABSTRACT

Snapping shrimp in the family Alpheidae are remarkably abundant in coral reef ecosystems worldwide. Those belonging in the second most speciose genus, *Synalpheus*, are usually small and reclusive, and their general morphology is notably uniform, yet the number of species included in this genus is staggeringly high, as is the intraspecific variability. All of these features have contributed to a poorly resolved taxonomic status of *Synalpheus*, as evidenced both by recurring lumping and splitting of species and by the lack of proper definition of several common species such as *S. longicarpus*, *S. pandionis*, and *S. brevicarpus*.

This study examined western Atlantic species of *Synalpheus* in the large and regionally dominant “Gambarelloides group of species”, an informal but widely used guild within the genus. Analysis of external anatomical features of preserved and live specimens allowed for the reassessment of morphological characters traditionally used in the taxonomy of *Synalpheus*, and incorporation of novel characters in the revision. The identity and validity of every species described from the western Atlantic has been reevaluated. Detailed ecological records and observations on live specimens under laboratory conditions yielded ancillary data useful in distinguishing the species. Seven new species are preliminarily described herein. Most of the western Atlantic species, namely 30 out of 40, including the seven new to science, belong in the Gambarelloides group. They bear a distinctive brush of setae on the dorsal surface of the dactyl of the minor first pereiopod and a coxal lamella on the pereiopods of the third pair. The brush of setae is used in feeding and appears related to their spongicolous habits. It is recommended that the Gambarelloides group of species should be recognized as a distinct subgenus within *Synalpheus*. A systematic account of 17 species with selected illustrations and color photographs is included, together with a dichotomous identification key.

The evolution of morphological characters was traced onto the current best reconstruction of the phylogenetic relationships among the species of the Gambarelloides group. The phylogenetic tree was obtained by analyzing molecular data from segments of two mitochondrial genes (COI and 16S) from 39 species of *Synalpheus*, with *Alpheus cylindricus* as the outgroup. The information content of the morphological characters for reconstructing the history of the genus was also evaluated. As suspected, most of the morphological characters studied bore a weak phylogenetic signal and homoplasies were frequent. Nevertheless, at least two characters provided consistent synapomorphies that define the Gambarelloides group of species: the brush of setae on the dorsal surface of the dactyl of the minor first chela, and the coxal lamella on the third pereiopods.

The study of the evolution of the genus *Synalpheus* is particularly interesting because of the high number of closely related species, their similar general ecological preferences with microhabitat specificity, and the variation in their social organization. This taxonomic and systematic reassessment of western Atlantic *Synalpheus* provides a solid taxonomy and an important frame of reference for future studies of biology of the genus *Synalpheus*. The clear taxonomic boundaries established here will be essential for robust hypothesis testing in evolutionary studies of these abundant and diverse shrimps.

*Synalpheus* SHRIMP FROM CARRIE BOW CAY, BELIZE.

SYSTEMATICS, PHYLOGENETICS AND BIOLOGICAL OBSERVATIONS

(CRUSTACEA: DECAPODA: ALPHEIDAE)

## General Introduction

Snapping shrimps in the genus *Synalpheus* Bate, 1888 are major components in coral reef and other marine ecosystems (Felder and Chaney 1979, Reed *et al.* 1982). They are common and abundant in coral crevices, as well as within numerous species of sponges (Beebe 1928, Pearse 1932, Bruce 1976, Duffy 1992). In general these shrimp are small and reclusive, but they often outnumber other cryptofaunal species (Pearse 1932, Rützler 1976). *Synalpheus* is an excellent subject for studies of a number of topics in evolutionary biology because of the profusion of closely related species with distinct ecological preferences and social organization that include pair-forming, as well as subsocial and eusocial aggregations (Beebe 1928, Duffy 1996a, 1998; Duffy and MacDonald 1999, Duffy 2003). Interestingly, the genus includes the only marine invertebrates wherein eusociality has been documented (Duffy 1996a, 1998, Duffy and MacDonald 1999). Given the abundance and diversity of species in the genus, it is remarkable that the systematic relationships and taxonomy of *Synalpheus* are still not well established. An improved phylogenetic and taxonomic framework for *Synalpheus* would facilitate studying the evolution and behavior in this taxon. Comparative analysis of characters should allow both the reconstruction of phylogenies as well as the establishment of a better classification (Mayr 1969).

### Diversity of *Synalpheus* species and intraspecific variability

Among the 28 currently recognized families of caridean shrimps, the Alpheidae Rafinesque, 1815 ranks fourth in the number of currently recognized genera, with a total of 37 (Chace and Kensley 1992, Holthuis 1993, Hayashi 1998, Kim 1998, Wicksten 1999, Anker and Iliffe 2000, Dworschak *et al.* 2000). The two most species-rich genera in the

family are *Alpheus* Fabricius, 1798 with more than 250 species (Kim and Abele 1988), and *Synalpheus* Bate, 1888 with more than 130 species (Chace 1988, Ríos, pers. obs.).

The remarkably uniform morphological appearance (Banner and Banner 1975) of the species of *Synalpheus* has resulted in a scarcity of consistent taxonomic characters. Considerable variability within single species has also caused much confusion, especially when the number of available specimens is small. In brief, the species of *Synalpheus* have often been separated by subtle differences that are not stable characters (Banner and Banner 1975; Chace 1972). This dissertation is intended to help resolve these problems.

### Historical review of *Synalpheus*

The Russian scientist Paulson (1875) first noticed that among what was known as “*Alpheus*”, there was a distinct group of species sharing a most important character: the absence of epipods on the pereopods. In *Alpheus*, epipods are present on the third maxilliped and the first four pairs of pereopods (Banner and Banner 1975) as hooked processes inserted laterally on the coxae; these processes are functionally associated with setobranchs on the immediately posterior pereopod, and both structures are involved in gill cleaning (Bauer 1979). Unfortunately, Paulson (1875) used the name “*Alpheus*” for the group lacking epipods while erecting *Alpheoides* to include the true *Alpheus*. According to De Man (1911), unaware of Paulson’s achievements, he had also created in 1888 a “group spinifrons” within the genus *Alpheus* for the species corresponding to the present *Synalpheus*. It was Spencer Bate (1888) who formally erected the genus *Synalpheus*. Ironically, the first species he included in his new genus, which became the type species for the genus, *Synalpheus falcatus* (= *S. comatularum*), had been previously described as *Alpheus comatularum* by Haswell (1882).

Henri Coutière (1897) provided the first extensive diagnosis that established unequivocally the identity of *Synalpheus* Bate. In his treatise on the Alpheidae, Coutière (1899) gave accurate diagnoses of the 16 genera included in that family at that time. The name *Synalpheus* Bate, 1888 was included on the Official List of Generic Names in Zoology in opinion 470 in 1957 (Holthuis 1993). Nevertheless, a sound definition for the genus is still not readily available (*vide* Verrill 1922, Banner and Banner 1975, and Chace 1988).

The most relevant publications regarding *Synalpheus* from the Caribbean region include Coutière (1909), Chace (1972), Christoffersen (1979), Dardeau (1984), and Duffy (1996c). The essential paper by Coutière (1909), originally in French and translated into English by Mary J. Rathbun, United States National Museum, was the first thorough revision of *Synalpheus* from the Americas. Remarkably, of more than 45 species and varieties included therein, Coutière (1909) retained only three species with their previous names, *i. e.* *Synalpheus brevicarpus* (Herrick, 1891), *S. longicarpus* (Herrick, 1891), and *S. minus* (Say, 1818). With regard to the material from both coasts of the American continent, Coutière (1909) assigned a new name to *S. lockingtoni*, and erected 20 new species and 20 subspecies. Two of his new species have names that had been previously published: *S. hemphilli* Coutière, 1908 and *S. pectiniger* Coutière, 1907. Coutière (1909) also included material from other parts of the world; he erected 11 new species, two new subspecies, and gave full specific status to *S. laevimanus parfaiti*.

Coutière (1908, 1909) divided the genus *Synalpheus* into six groups of species according to morphological, ecological, and evolutionary features. Banner and Banner (1975) reassessed the definitions of the groups, and concluded that only three of them “may be coherent enough to continue to be recognized”, namely the Comatularum, the

Brevicarpus, and the Gambarelloides. Species belonging in the Gambarelloides group are morphologically characterized mainly by a brush of thickly packed long setae on the upper surface of the dactyl of the minor first chela (Coutière 1908, 1909; *vide* figure 0-1); these setae are distally curved and arranged in transverse parallel rows. Interestingly, although the group takes the name from a Mediterranean species, *Synalpheus gambarelloides*, the Gambarelloides species are known almost exclusively from the Caribbean region, where they constitute the majority of the species in the genus *Synalpheus*. Only seven putative Gambarelloides species are known from outside the western Atlantic: *S. parfaiti* from west Africa (Crosnier and Forest 1966); *S. gambarelloides* from the Mediterranean and East Africa, *S. crosnieri*, *S. sladeni*, and *S. spongicola* from East Africa (Banner and Banner 1983); and *S. mulegensis* and *S. occidentalis* from the Gulf of California (Wicksten 1994). In contrast, 30 of 40 species of *Synalpheus* known from the western Atlantic belong in the Gambarelloides group. These figures will possibly change when other parts of the world are more carefully surveyed, but for the time being, it appears likely that the Caribbean region is the center of dispersion for the Gambarelloides group.

Chace (1972) studied the shrimps collected during four expeditions to the Caribbean region organized by the Smithsonian Institution from 1956 to 1960. Summarizing therein the West Indian shallow-water species, he included 28 species of *Synalpheus*, and described four as new, explicitly stating that he was not recognizing most of the numerous subspecies described by Coutière (1909) because “many are sympatric with the typical form of the species concerned, and there seems little doubt that most of them display only varietal differences” (Chace 1972).

Christoffersen (1979) studied eight species of *Synalpheus* with abundant material

collected mainly by the R/V *CALYPSO* in South American waters. In disagreement with Chace (1972), he listed five new synonyms for *S. brooksi*, and three for *S. longicarpus*.

In reviewing 19 species of *Synalpheus* from the Gambarelloides group, Dardeau (1984) gave a detailed account of the 11 species he recorded from the Gulf of Mexico, including the description of a new species. In that paper, Dardeau disproved some of Christoffersen's (1979) results, and resurrected *S. bousfieldi*, *S. herricki*, and *S. pandionis*.

Using a multidisciplinary approach, Duffy (1996c) brought genetic, ecological and morphometric data to the taxonomy of the genus *Synalpheus*. Analyzing several populations closely related to *S. rathbunae*, he distinguished four distinct species, and suggested that within the genus many sympatric forms might prove to be good biological species. Subsequently, he erected *S. regalis* for one of the forms recognized in his study (Duffy 1996b).

Additional taxonomic works on *Synalpheus* from the Caribbean include: Say (1818), Herrick (1891), Coutière (1907, 1908, 1910), Schmitt (1924, 1933), Verrill (1922), Armstrong (1949), Pequegnat and Heard (1979), Dardeau (1986), Duffy (1998), and Ríos and Duffy (1999).

### Statement of purpose

The general purpose of this dissertation is to carefully study the external anatomy of *Synalpheus* (Fig. 0-1) to assess its bearing on the taxonomy of the western Atlantic species in the Gambarelloides group, and to appraise the value of morphological characters in reconstructing the phylogenetic relations among species in this group. This research is intended not only as a contribution to improving alpha taxonomy, via the rigorous formal



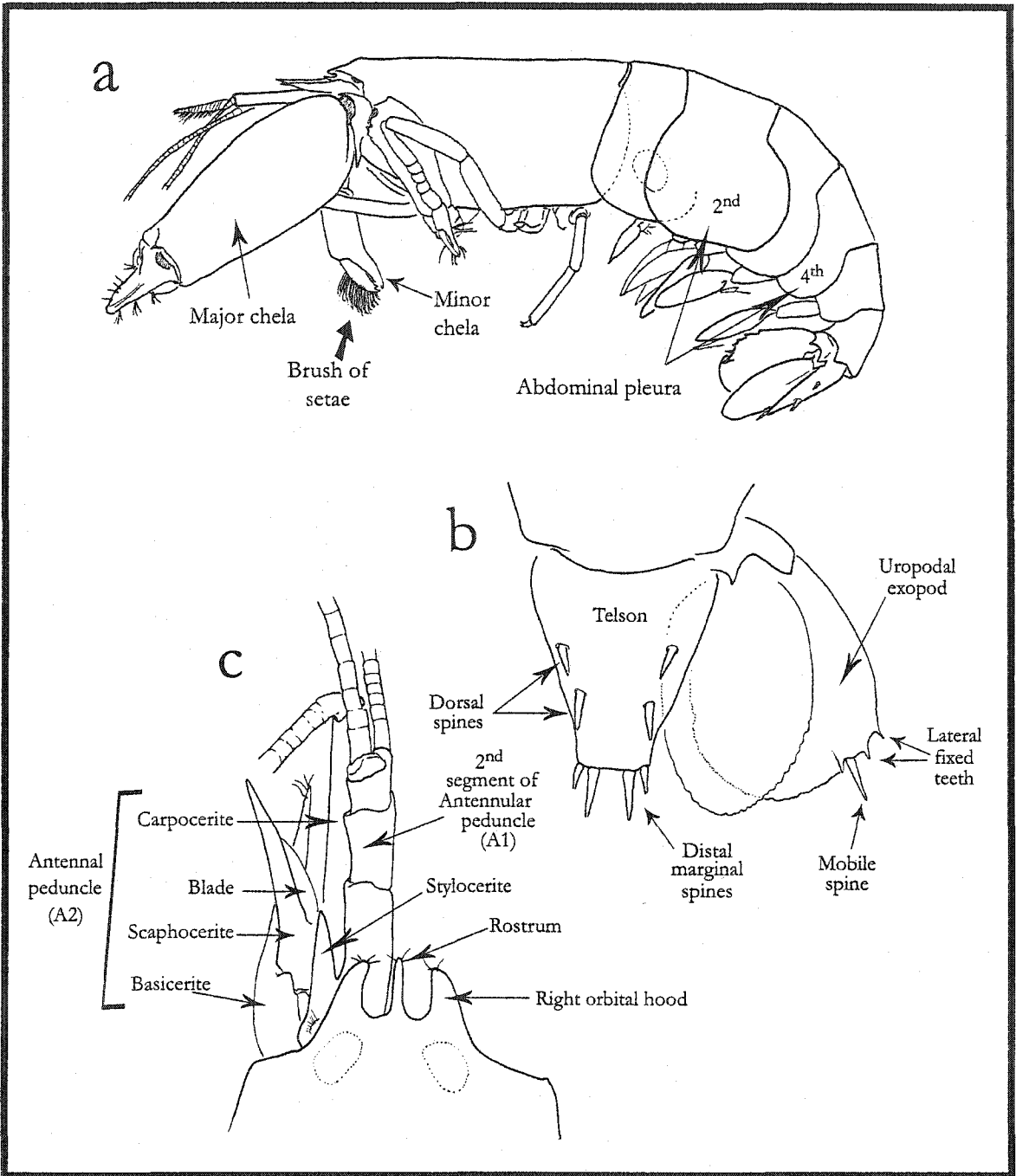


Figure 0-1. Schematic drawings of a *Synalpheus* shrimp showing important structures used in taxonomy: a, ovigerous female, lateral view; b, tail fan with left uropod omitted, dorsal view; c, anterior region of carapace with left antennal (A2) and antennular (A1) peduncles, dorsal view.

description of new species, but also, as an exploration of the value of morphology in reconstructing the current phylogenetic relationships of these shrimp.

As an example of alpha taxonomic work, Chapter one is the description of *S. williamsi* Ríos and Duffy, 1999 that has already been published. Chapter two is an updated catalogue of the 32 morpho-species of *Synalpheus* in the Gambarelloides group that I was able to distinguish, based primarily on material collected in the vicinity of Carrie Bow Cay, Belize. That chapter includes alpha taxonomy in the form of preliminary descriptions of six unnamed species, line drawings and color photographs for selected species, and a revised identification key. Chapter three is the preliminary description of an additional new species from Panama, *Synalpheus* sp.7, whose provisional denomination follows the serial numbers from chapter two. In Chapter four I analyze the phylogenetic information of 54 morphological characters, by mapping them onto an extrinsic tree produced after the partial sequencing of two genes, COI and 16S (Morrison, Ríos and Duffy, in press). The purpose was to rigorously assess the value of morphological characters in the classification and taxonomy of *Synalpheus* in the Gambarelloides group of species.

I conclude with summary remarks and ideas for future work (Chapter five).

---

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## CHAPTER ONE

### Description of *Synalpheus williamsi*, a new species of sponge-dwelling shrimp (Crustacea: Decapoda: Alpheidae), with remarks on its first larval stage.\*

**Abstract-** A new species of *Synalpheus* is described based on specimens collected from sponges in Belize and the Atlantic coast of Panamá. The new species, *S. williamsi*, is most similar morphologically to *S. goodei* Coutière, but the two species are consistently different in several morphological and larval features, and occupy distinct species of sponges. The shape of the major chela and of the uropodal exopods are the most reliable morphological characters that distinguish the two species. The first larval stage, a zoea I, was obtained from an ovigerous female of the new species. The zoea I is similar to that of *S. neomeris* (De Man), *S. triunguiculatus* (Paulson), *S. tumidomanus* (Paulson), and *S. scaphoceris* Coutière, in lacking pleopods and chelae, but can be distinguished by the presence of an acute projection on the pterygostomian corner.

**Resumen-** Se describe una nueva especie de *Synalpheus* en base a especímenes recolectados dentro de esponjas en Belice y la costa Atlántica de Panamá. La nueva especie, *Synalpheus williamsi*, es muy parecida a *S. goodei* Coutière, pero posee distintas características ecológicas, morfológicas y larvarias. Estas dos especies de *Synalpheus* habitan distintas especies de esponjas. Los caracteres morfológicos más confiables para distinguirlas son la forma de la quela mayor y de los exópodos uropodales. De una hembra ovígera se obtuvo la primera fase larvaria, una zoea I desprovista de pleópodos y de quelas. La zoea I de la nueva especie es muy similar a la de *S. neomeris* (De Man), *S. triunguiculatus* (Paulson), *S. tumidomanus* (Paulson), y *S. scaphoceris* Coutière, pero se distingue de ellas por la presencia de una proyección pterigostomiana aguda en el caparazón.

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During the course of collections made over several years in Belize and on the Atlantic coast of Panamá, we obtained a number of shrimps of a sponge-dwelling *Synalpheus* species morphologically similar to *S. goodei* Coutière, 1909. Specimens were collected from living sponges taken by SCUBA from various depths (1-15 m) on the outer reef ridge at the Smithsonian Institution's field station on Carrie Bow Cay, Belize (16°48' N, 88°05' W), and from Ulagsukun, Pico Feo, and Mamitupo reefs near the Smithsonian Tropical Research

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\*Ríos, R. and J. E. Duffy 1999 Description of *Synalpheus williamsi*, a new species of sponge-dwelling shrimp (Crustacea: Decapoda: Alpheidae), with remarks on its first larval stage. Proceedings of the Biological Society of Washington, 112: 541-552.

Institute's (STRI) field station in the San Blas Islands, on the Atlantic coast of Panamá (9° 34' N, 78° 58' W). Specimens from both areas were collected from the internal canals of the midnight-blue sponge *Hymeniacidon caerulea* Pulitzer-Finali, 1986, although one was associated with an unidentified orange encrusting sponge of tubular shape. Four specimens were collected free from any host, and had probably left their host sponges during sample handling. Usually, a heterosexual pair or a single adult was found in a same sponge. Here we describe these specimens as *Synalpheus williamsi*, new species. We also include a diagnosis of the first zoeal stage of this species hatched in the laboratory. Material is deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D. C. (USNM); Colección Nacional de Crustáceos from the Instituto de Biología UNAM, México (CNCR), the Museum National d'Histoire Naturelle, Paris (MNHN), and in the Virginia Institute of Marine Science (VIMS). Measurements indicated are of carapace length including rostrum.

### *Synalpheus williamsi*, new species

Figs. 1-1 through 1-6

**Type specimens-** Holotype ♂, 3.6 mm (USNM-276158), allotype ovigerous ♀, 4.5 mm (USNM-276159), Carrie Bow Cay, Belize, 13 Jun 1996, from canals of same specimen of midnight-blue sponge *Hymeniacidon caerulea*, 18 m.- Paratypes: ♂, 4.4 mm, 2 ovigerous ♀♀, 4.3, 4.8 mm (USNM-276160), Carrie Bow Cay, Belize, 4 Apr 1993, from canals of same specimen of midnight-blue sponge *H. caerulea*, 13 m; Paratype ♂, 2.3 mm (CNCR 17987) Carrie Bow Cay, Belize, 12 Jun 1996, from canals of midnight-blue sponge *H. caerulea*, 18 m; Paratype ♂, 3.7 mm (MNHN-Na 13561) Ulagsukun Reef, Panamá, 17 Jan 1991, from canals of midnight-blue sponge *H. caerulea*.

**Additional specimens examined (non paratypes)-** Belize: Carrie Bow Cay, 5 Apr 1993, 2 ♂♂, 2.9, 3.8 mm (VIMS); 18 Aug 1994, ♂, 3.5 mm (VIMS); 26 Aug 1994, ♂, 4.7 mm (VIMS), zoea larvae (USNM-276161); in midnight-blue sponge *H. caerulea*. Panamá: Ulagsukun Reef, 18 Jan 1991 ovigerous ♀, 4.2 mm (VIMS); 10 Nov 1992, ♂, 3.7 mm (VIMS); in midnight-blue sponge *H. caerulea*, 1 m; Pico Feo Reef, 18 Jan 1991, ♂, 3.4 mm, ovigerous ♀, 4.2 mm (VIMS), in midnight-blue sponge *H. caerulea*; San Blas Islands: 1991, ♂, 4.3 mm (VIMS); Mamitupo Reef: 19 Jan 1991, ♂, 4.1 mm (VIMS), in orange tubular sponge.

**Description of holotype-** Body form subcylindrical. Carapace smooth, with sparse short simple setae. Rostrum (Figs. 1-1 a, d, e) slender, distally upturned, slightly overreaching orbital teeth, not reaching to distal margin of first segment of antennular peduncle; dorsally carinated; ventrally produced into small longitudinal keel, but without true orbitorostral process. Ocular hoods (Figs. 1-1 a, d, e) dorsally convex, separated from rostral carina by broad depressions; triangular ocular teeth and rostrum with few apical setae; adrostral notches broadly rounded. Pterygostomian corner (Fig. 1-1 b) produced into bluntly acute angle. Posterior margin (Figs. 1-2 a, d) with distinct cardiac notch.

Abdomen with sparse simple setae; pleuron of first somite (Fig. 1-2 d) with anterior corner almost in right angle, ventral margin sinuous and posteriorly bearing a blunt strongly hooked tooth directed anteriorly; second pleura broadly rounded anteriorly, with ventral margin slightly concave and posterior corner rounded, but with widely obtuse projection behind 3/4 of length; third to fifth pleura anteriorly and posteriorly obtuse, ventral margin triangular with apex progressively displaced posteriorly; sixth abdominal segment (Fig. 1-2 a) with bluntly acute projection on posteroventral margin, shallow curved inferior concavity, triangular lateral lobe with convex sides, shallow obtuse upper emargination, and convex

dorsal margin slightly overhanging telson. Telson (Fig. 1-1 c) subtriangular, truncate, proximal margin slightly more than twice as wide as distal margin; lateral margins slightly convex just as far as distal pair of dorsal spines, then slightly concave; dorsal surface with mesial shallow depression and 2 pairs of dorsal spines, anterior pair situated slightly anterior to proximal third of length of telson, posterior pair of dorsal spines at second third of length of telson; distal margin arcuate, posterolateral corners not projected, 2 pairs of flanking distal movable spines, lateral pair shorter than innermost; mesial gap wider than combined bases of both pairs of spines, with 2 tufts of 3 erect setae on dorsal surface mesially adjacent to inner spines, and single row of 8 more conspicuous, posteriorly directed plumose setae of similar size, emerging from under mesial distal lobe.

Stylocerite (Figs. 1-1 a, d) slender, with mesial side slightly concave, barely overreaching distal margin of basal article of antennular peduncle; this latter with lateral fan of setae proximally on dorsal face; second and third segments of antennular peduncle decreasing in length. Upper flagellum (Figs. 1-1 a, b) biramous, rami fused for 5 segments; lower ramus shorter, with 3 groups of aesthetascs on ventral face, and 4 and 5 additional groups posteriorly, upper ramus with 12 and 15 segments (left and right side, respectively). Lower flagellum normal, longer than upper.

Basicerite (Figs. 1-1 a, b, d) with acute dorsolateral projection, and longer acute ventrolateral spine overreaching tip of stylocerite; scaphocerite blade slightly reduced reaching to distal edge of antennular peduncle, narrower at base than lateral spine, which is robust, acute, with slightly concave lateral margin, and clearly overreaching antennular peduncle. Carpocerite (Figs. 1-1 b, d) about 7 times as long as wide when viewed laterally, overreaching tip of lateral spine of scaphocerite.

Exopod of third maxilliped (Fig. 1-3 f) not overreaching antepenultimate article, tip of ultimate segment (Fig. 1-3 g) with circle of 7 strong blunt spines finely denticulate on proximal half of inner face. Remaining mouthparts as figured from paratypes (Figs. 1-3 a-e).

Major first pereiopod (Figs. 1-4 a, b, c) massive, subcylindrical, with few sparse setae; palm about 1.75 times longer than wide, dorsodistal margin with blunt prominence overhanging insertion of dactyl, and bearing subterminal, ventrally directed, acute spine. Dactyl 0.3 times as long as palm, strongly compressed, dorsal margin broadly semicircular in lateral view (Fig. 1-4 b), cutting edge almost flat with discrete blunt tip, internal face opposing outer face of pollex when closed. Pollex 0.7 times as long as dactyl, deeply excavated proximally to receive dactylar molar process, in ventral view (Fig. 1-4 g), thick, triangular, with accessory subdistal obtuse projection on outer face, flanking outer face of dactyl when closed. Carpus cup-shaped, short and broad. Merus, about 0.8 times as long as height of palm, nearly triangular in cross section, inner edges slightly concave, outer convex, lower side flattened, with lamellar triangular projection on distal outer corner, upper side clearly convex.

Minor first pereiopod (Fig. 1-4 d) slightly compressed. Palm about 1.7 times longer than high. Dactyl 0.7 times as long as palm, with several tufts of regular setae; extensor margin convex, with 2 longitudinal series of transverse parallel rows of setae distally curved towards tip of dactyl, inner series composed of about 12 rows, first row at start of second third of dactyl, last row at end of fourth fifth, shorter outer series, with first row opposing fifth row of inner series, setae similar in shape, length, and orientation, but slightly thinner; dactyl flexor margin excavated (Fig. 1-4 e), tip with strong tooth flanked by two accessory blunt projections. Pollex with sinuous lower margin, sparse tufts of setae, strong apical

tooth (Fig. 1-4 f) continued backward into oblique widely convex blade. Carpus cup-shaped, about 0.5 times as long as palm; 1.2 times higher distally than mesial length in lateral view; upper and lower margins distally expanded over proximal portions of palm. Merus 1.5 times as long as palm, 2.5 times longer than maximum width; almost triangular in cross section; distal outer corner flared, without true spine.

Second pereopod (Fig. 1-4 h) more slender than all others. Fingers with strong tufts of setae, slightly more than 1.3 times as long as palm, latter 1.4 times longer than high. Carpus composed of 5 articles with ratio 4.5:1:1:1:2, second through fourth equally as long as high. Merus about 5.3 times longer than wide, and 0.9 times as long as carpus. Ischium four times longer than wide, and 0.7 times as long as merus.

Third pereopod (Fig. 1-5 a), strongest of posterior legs. Dactyl (Fig. 1-5 d) biunguiculate, slightly longer than width of propodus, flexor margin concave. Propodus 6.3 times longer than wide, flexor margin with a longitudinal series of 7 strong movable spines and one terminal pair of movable spines flanking base of dactyl. Carpus 2.6 times longer than wide, extensor distal margin projected over propodus, strong movable spine on distal flexor margin. Merus 4.4 times longer than wide, unarmed. Ischium unarmed.

Fourth pereopod (Figs. 1-5 b, e) very similar to third, but slightly weaker.

Fifth pereopod (Figs. 1-5 c, f) weaker than fourth, with following slight differences, propodus with only two or three spines on flexor margin besides distal pair, and about five combs of stout setae transversely arranged on distal half of posterior face; carpus without spine.

Endopod of first pleopod (Fig. 1-2 e) not as long as width of exopod, with few apical setae (Fig. 1-2 f). Second pleopod (Fig. 1-2 g) without appendix masculina. Pleopods 2-5

with appendix interna.

Uropodal exopod (Fig. 1-1 c) with 5 strong distolateral teeth, longer movable spine and acute mesial tooth. Diaeresis present, distinct.

**Color-** Live specimens were translucent faint gold to golden brown, with tip of chelae (fingers and distal part of palm included) of first pereopods bright orange to red, second legs golden, third to fifth transparent, and traces of blue in the gut and in the branchiae. These traces were the same dark blue as the host sponge, and they still can be seen in some of the preserved specimens.

**Variations-** The few discrepancies between the illustrations, from a male paratype, and the holotype are most probably due to the larger size of the figured paratype. The greater development of the endopod on the first pleopod (Fig. 1-2 f) could be related to different stages of sexual maturity. Regarding sexual dimorphism, the most striking female characters are the broadly rounded shape of the first to fourth pleurae (Fig. 1-2 a), the larger endopod of the first pleopod (Fig. 1-2 b), and the insertion of the appendix interna beyond the midpoint in the remaining pleopods (Fig. 1-2 c).

On the tip of third maxilliped, eight or seven spines is the most frequent formula, (as in the holotype), but the allotype has nine spines on one side and ten on the other. The number of immovable teeth on the lateral margin of the uropodal exopod varies from three to six, with a mode of four; this variation apparently relates to size and perhaps sex, considering that the smaller specimens have fewer teeth, and that the only two specimens with six teeth were males.

**Eggs and larva-** Eggs measure 0.9-1.0 mm long, and about 0.6 mm wide. One ovigerous female released larvae in the laboratory. Seven larvae were recovered swimming

freely, but no attempts were made to raise them beyond the first stage. They were both preserved and stored in ethanol along with two eggs and another larva with half its body still in the egg case.

**Description of zoea I-** Carapace subcylindrical (Fig. 1-6 a), pterygostomian corner projected into acute spine, low bump on middorsal line, and angular projection proximal to depression at base of rostrum; latter, broadly triangular, pointed, directed downwards, shorter than, and somewhat hidden by ocular peduncles; eyes not covered by carapace.

Antennular peduncle with 3 segments. Antennal scale with 2 outer plumose setae, outer apical spine, and 9 plumose setae on inner and distal margins; endopod reaching to first inner seta on scale, entire, with one strong and one small apical seta. Maxillae and mandible buds present. All maxillipeds with well developed endopods and strong exopods, but setae present only on exopods.

First to fourth pairs of pereopods biramous, without apparent segmentation, exopods without setae. Third and fourth pereopods rudimentary, folded anteriorly against thorax. Fifth pair, long, turned forwards, uniramous, without setae.

Abdomen with sixth segment not clearly separated from telson. Pleopods absent. Uropods fused with telson. Telson (Fig. 1-6 b), broad, bilobate, with 7 + 7 setae, outer 2 pairs feathered on inner side only, remaining 5 pairs plumose on both sides, innermost pair less than 0.25 as long as adjacent.

**Ecology-** Most specimens of the new species, *S. williamsi*, came from internal canals of the midnight-blue sponge *Hymeniacidon caerulea*. In a few cases (<25 %) we were not able to record the exact origin of our specimens, since they were found among debris in sampling containers. Only once did we collect a specimen (male) of *S. williamsi*, new species, from an



unidentified orange encrusting sponge of tubular shape that was clearly different from *H. caerulea*.

Traces of blue in the gut of some specimens, and the anecdotal record in our field notes of a voided fecal pellet containing sponge spicules, are suggestive of a parasitic relation between the shrimp and the sponge.

**Etymology-** It is an honor and pleasure to name this species after Dr. Austin B. Williams, National Oceanic and Atmospheric Administration, National Marine Fisheries Service Systematics Laboratory, National Museum of Natural History, Smithsonian Institution, Washington, D. C. This is in appreciation for his many important contributions to the knowledge of decapod crustaceans, and in recognition of his personal generosity and integrity.

**Remarks-** *Synalpheus williamsi*, new species, is morphologically similar to *S. goodei* Coutière, but the following characteristics of the latter serve to distinguish the two species: the blade on the scaphocerite is more reduced, the pollex on the major chela is longer and without an accessory lateral emargination (best seen in ventral view), the minor chela is more elongate, the distal margin of the telson is narrower, the lateral margin of the uropodal exopod has more fixed spines and has a noticeably stronger inner spine, adjacent to the movable one (see Coutière 1909, and Dardeau 1984). Also, unlike the new species, the first larva of *S. goodei* hatches at a more advanced stage with both pairs of chelae and pleopods present (Gurney 1949).

Among the 12 species of *Synalpheus* whose first larva has been described or figured, the zoea I from the new species, *S. williamsi*, is most similar to that of *S. neomeris* (De Man, 1888), *S. triunguiculatus* (Paulson, 1875), *S. tumidomanus* (Paulson, 1875), and *S. scaphoceris*

Coutière, 1910, but it can be readily distinguished by the acute projection of the pterygostomial corner; additionally, the first zoea of *S. scaphoceris* has the sixth abdominal somite clearly distinct (Dardeau 1986: fig. 3b). Lack of pleopods and chelae on the first pair of pereopods is suggestive of a normal development pattern, i. e., not abbreviated nor direct as has been documented for other species of *Synalpheus* (see Knowlton 1973, and Bhuti et al. 1977).

As in the case of *S. gambarelloides* (Nardo, 1847), and probably *S. longicarpus* (Herrick, 1891), recorded by Rützel (1976) and Erdman & Blake (1987) respectively, the new species, *S. williamsi*, appears to be a parasitic endobiont of sponges; more careful observations on live specimens might provide conclusive evidence on its diet.

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Figure 1-1. *Synalpheus williamsi*, new species. Paratype male 4.4 mm (USNM 276160): a, anterior region of carapace and cephalic appendages, dorsal view; b, same, lateral view; c, telson and uropods, dorsal view. Paratype ovigerous female 4.3 mm (USNM276160): d, anterior region of carapace and cephalic appendages, dorsal view; e, anterior region of carapace, lateroventral view. Scale bar = 1 mm for a, b, d, e, and 0.72 mm for c.

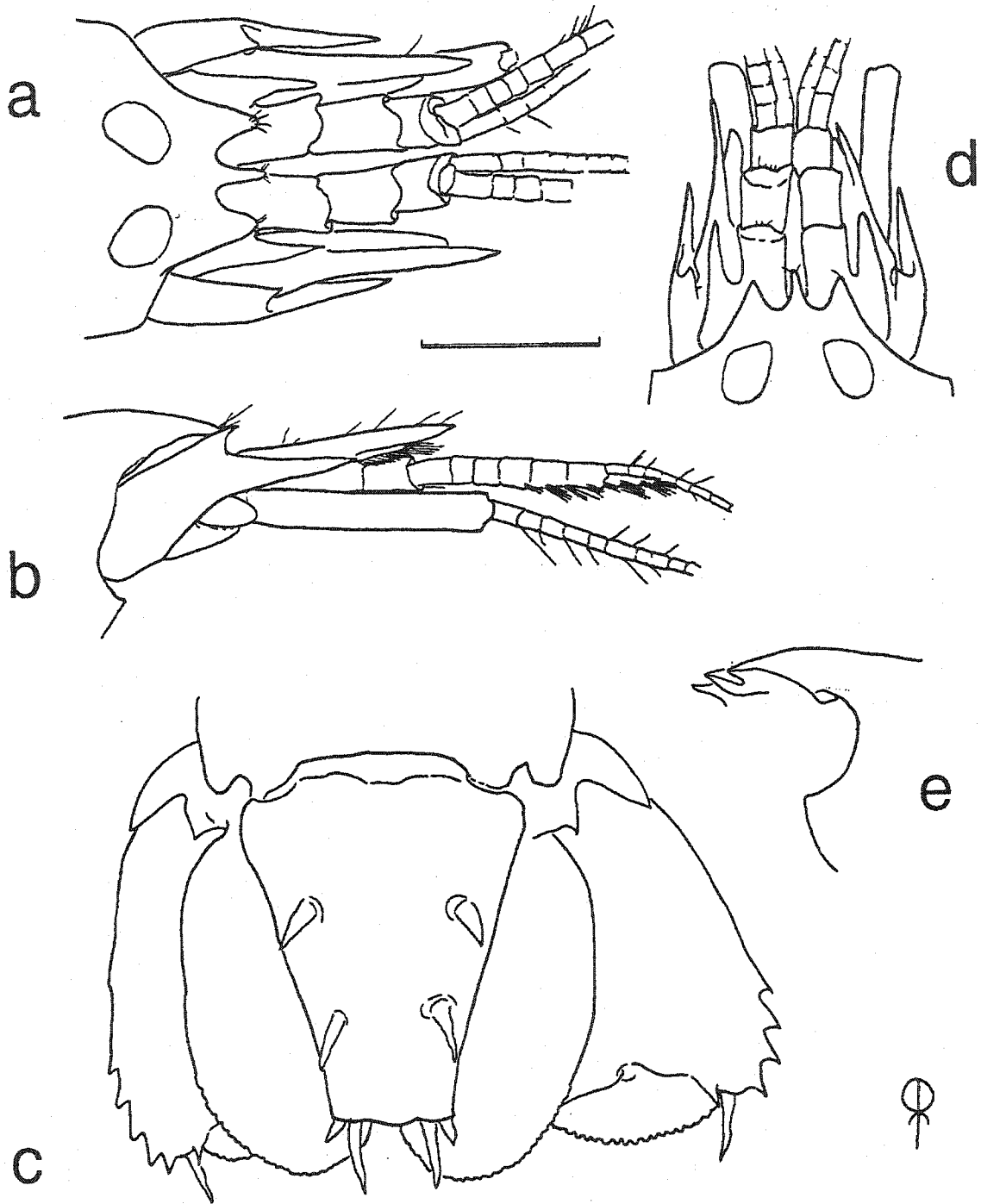


Figure 1-2. *Synalpheus williamsi*, new species. Paratype ovigerous female 4.8 mm (USNM 276160): a, abdomen with one egg, lateral view; b, first pleopod; c, second pleopod. Paratype male 4.4 mm (USNM 276160): d, first 5 segments of abdomen, lateral view; e, first pleopod; f, same, detail of endopod; g, second pleopod. Scale bar = 2.2 mm for a, d, 1 mm for b, c, e, g, and 0.31 mm for f.

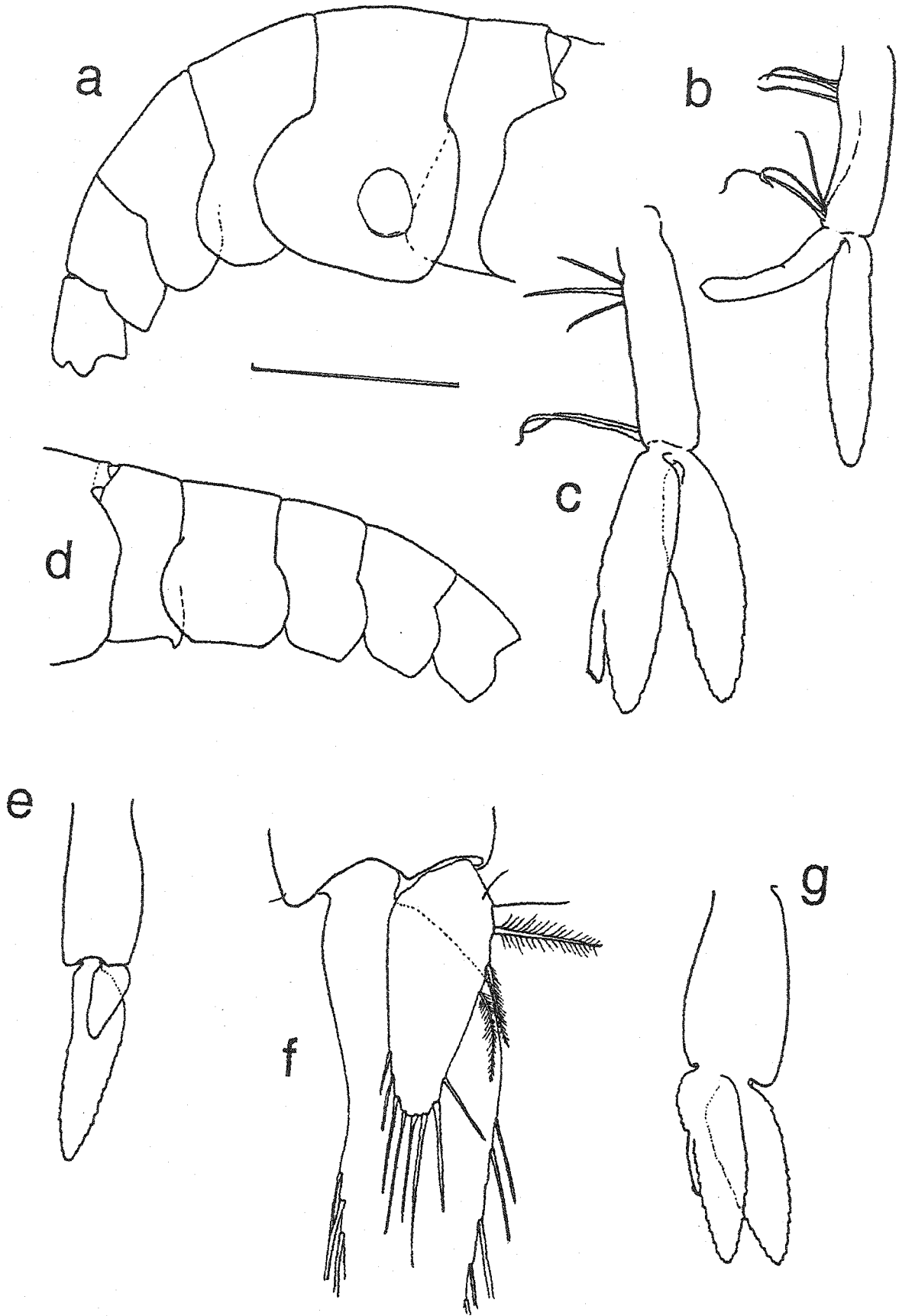




Figure 1-3. *Synalpheus williamsi*, new species. Mouthparts. Paratype male 4.4 mm (USNM 276160): a, mandible; b, first maxilla; c, second maxilla; d, first maxilliped; e, second maxilliped. Paratype ovigerous female 4.3 mm (USNM 276160): f, third maxilliped; g, same, detail of tip. Scale bar = 0.5 mm for a, b, c, d, e, 1 mm for f, and 0.25 mm for g.

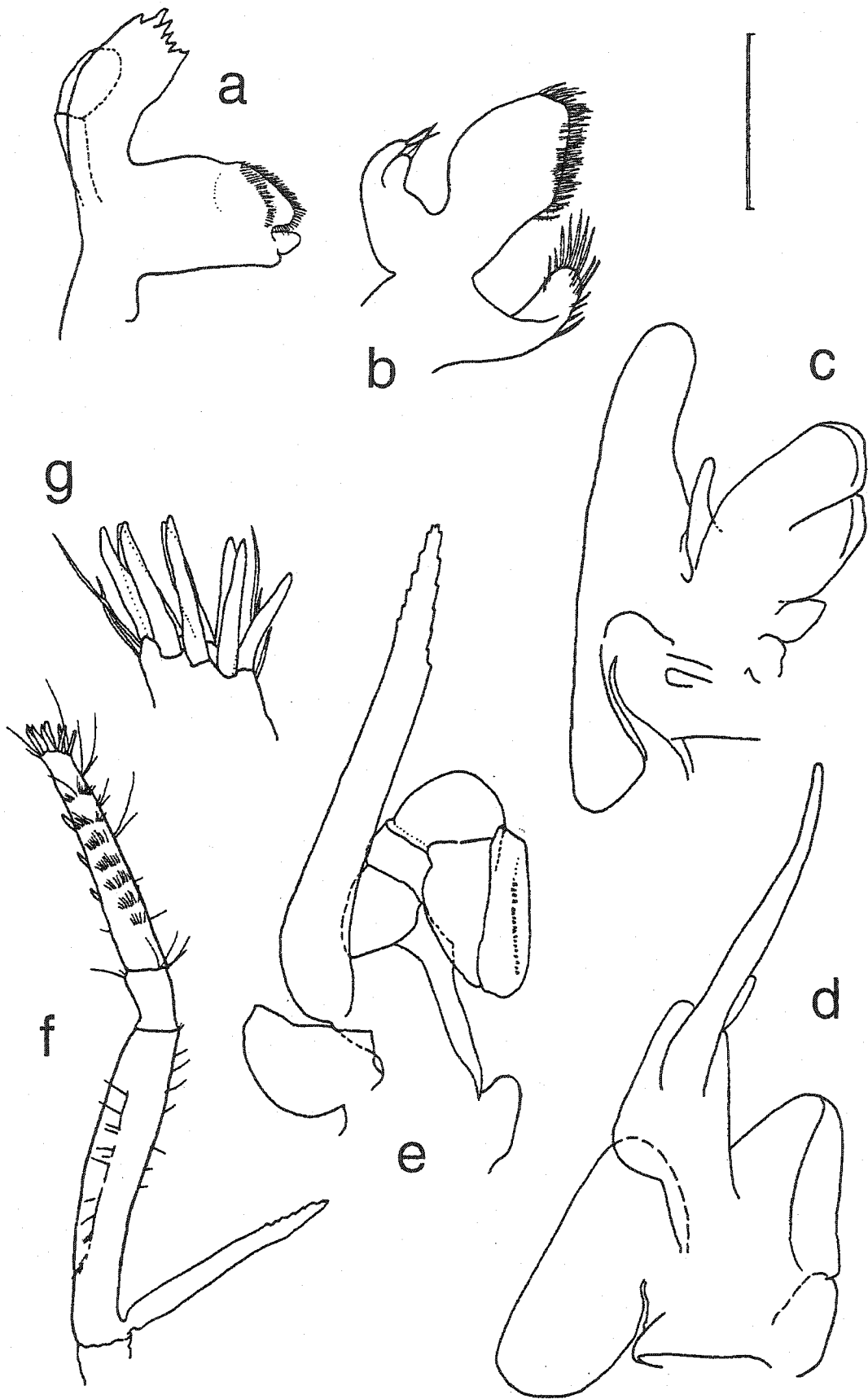


Figure 1-4. *Synalpheus williamsi*, new species. Paratype male 4.4 mm (USNM 276160): a, major first pereiopod in lateral view; c, chela of same, dorsal view; g, same, tip of pollex, ventral view; h, second pereiopod. Paratype ovigerous female 4.3 mm (USNM 276160): b, anterior portion of major first pereiopod, external face, lateral view; d, minor first pereiopod, lateral view; e, distal portion of same, lateroventral view; f, same, detail of tip, frontolateral view. Scale bar = 2.5 mm for a, 2.2 mm for b, c, 1 mm for d, 1.4 mm for e, g, 0.2 mm for f, and 2 mm for h.

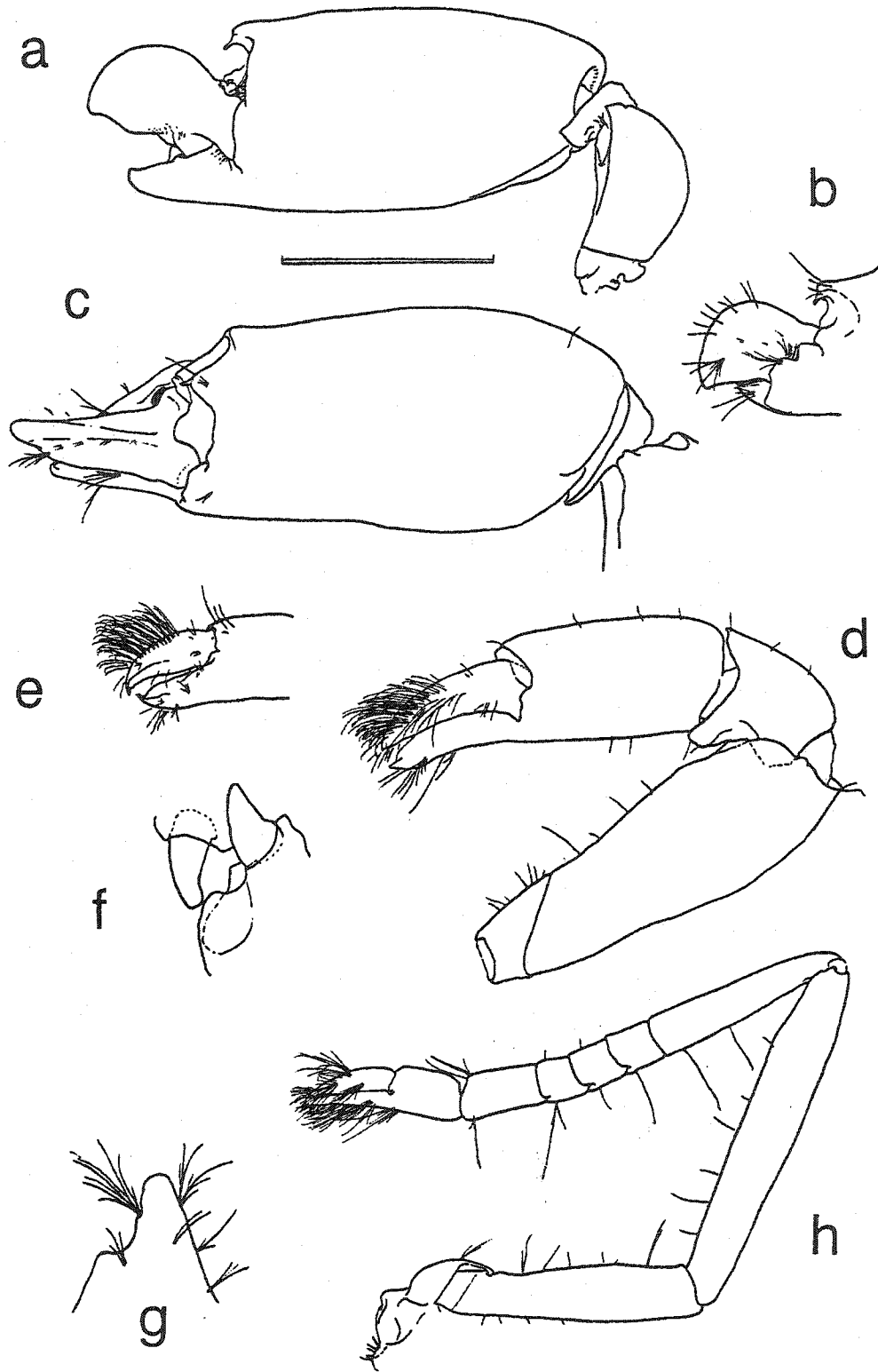


Figure 1-5. *Synalpheus williamsi*, new species. Paratype male 4.4 mm (USNM 276160): a, third pereopod; b, fourth pereopod; c, fifth pereopod; d, detail of distal portion of third pereopod; e, detail of distal portion of fourth pereopod; f, detail of distal portion of fifth pereopod. Scale bar = 1 mm for a, b, c, and 0.31 mm for d, e, f.

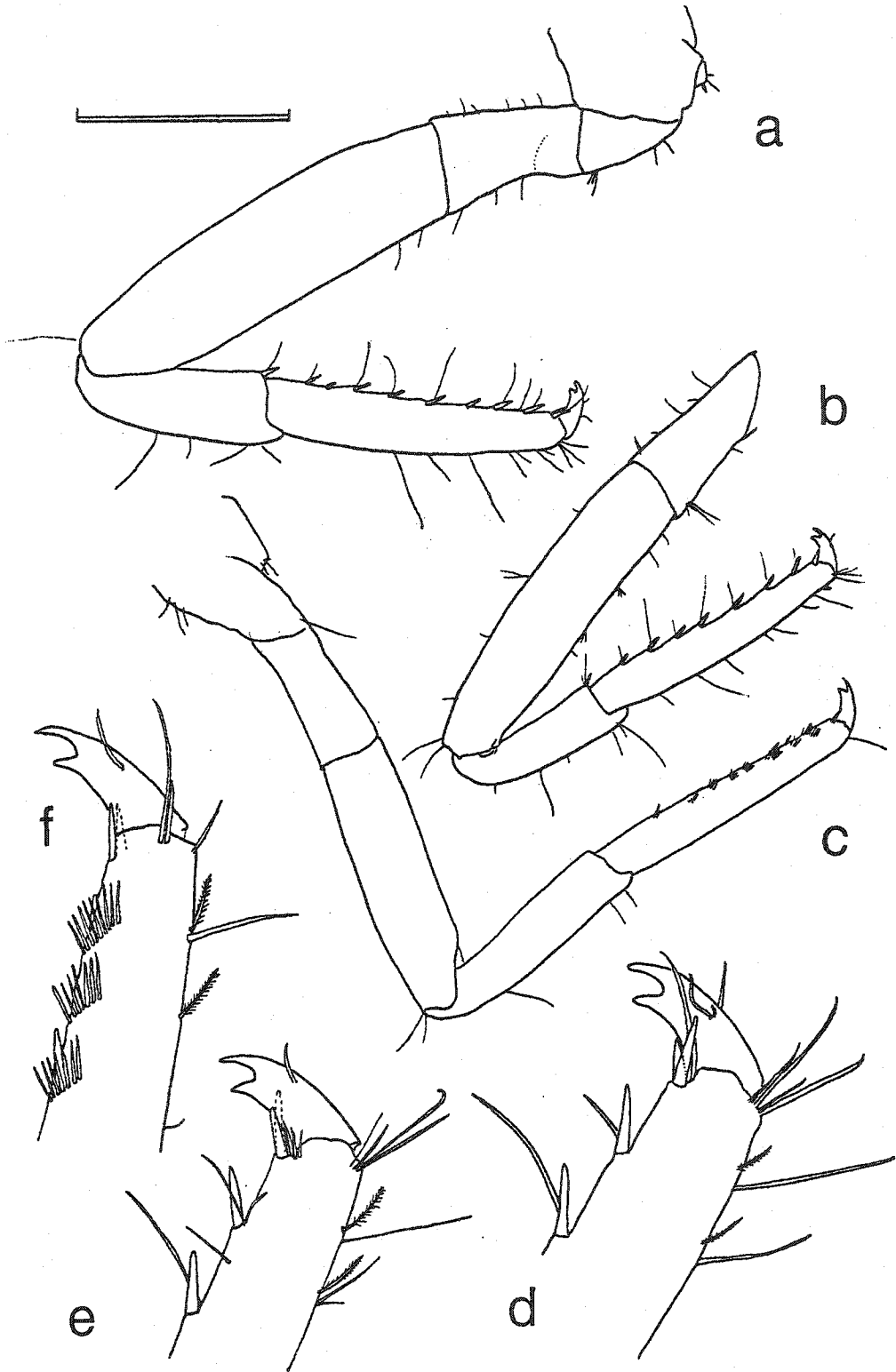
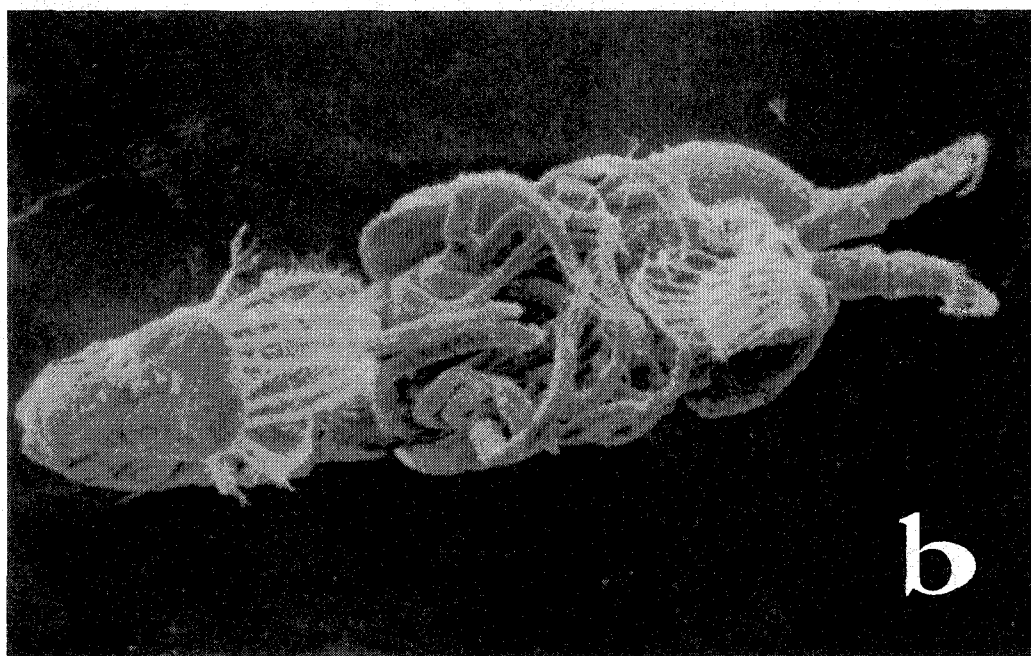
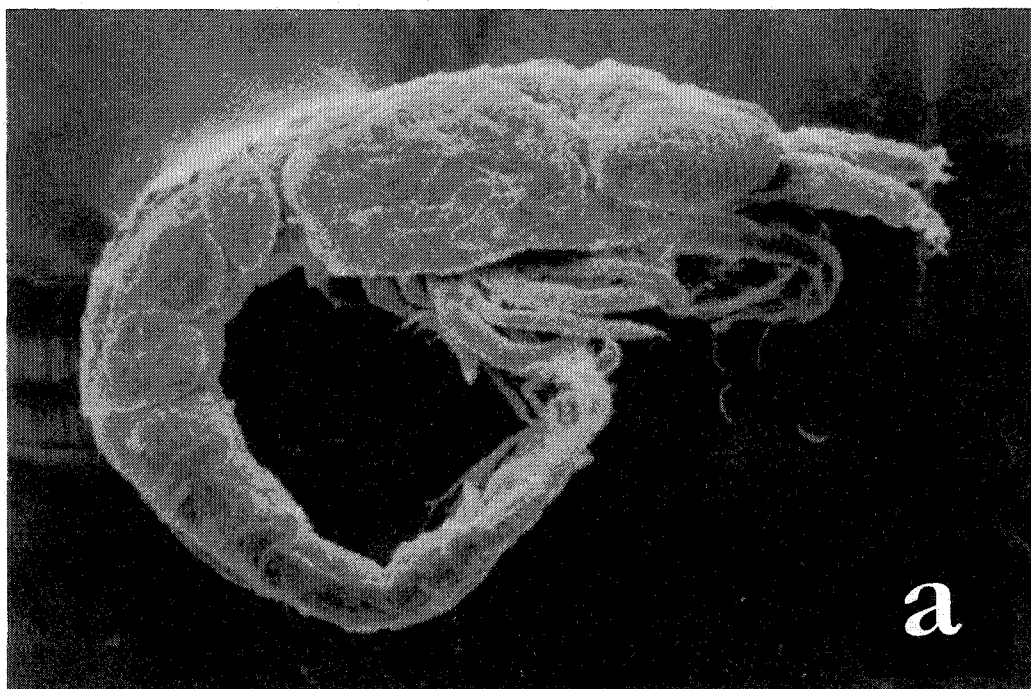


Figure 1-6. *Synalpheus williamsi*, new species. Scanning electron micrographs of first zoea stage: a, lateral view; b, ventral view. Magnification = 71 X.





## CHAPTER TWO

### Systematics of *Synalpheus* Bate, 1888 from Carrie Bow Cay, Belize (Crustacea: Decapoda: Alpheidae)

**Abstract-** This is a revision of the taxonomy and comparative morphology of snapping shrimp in the Gambarelloides group of species within the genus *Synalpheus* Bate, 1888 (Decapoda: Alpheidae), collected mainly in the area surrounding the Smithsonian Institution marine field station at Carrie Bow Cay, Belize. More than 70 % of the western Atlantic species belong in the Gambarelloides group, distinguished by a brush of setae on the dorsal surface of the dactyl of the minor first pereiopod, and the habit of association with living sponges. Also, considering their zoogeographic distribution, which is mostly restricted to the western Atlantic, the Gambarelloides species appear to be a natural group regardless of a lack of formal taxonomic recognition. A meticulous exploration of the external morphology of most species in this group resulted in the separation of at least 32 species, including six new to science, which are preliminarily described herein. A closer examination of the type material from most species has provided additional criteria with which to discriminate better the majority of the common species, including *S. brooksi*, *S. goodei*, *S. mcclendoni*, *S. pandionis*, and *S. sanctithomae*. In the case of *S. longicarpus*, whose holotype has been long suspected as nonexistent, the original description and figures proved accurate enough to allow for a positive identification of several specimens from Belize. Hitherto unknown males of *S. androsi* and *S. brevifrons* appeared several times in the examined material and are briefly diagnosed. *Synalpheus osburni* Schmitt, still known only from the holotype, is removed from the synonymy of *S. goodei*, and recorded as a valid species.

Detailed information on microhabitat, recorded while SCUBA diving, enable identification of a rather narrow range of sponge hosts for most of the *Synalpheus* species. Figures and color pictures of selected species are included, as well as an amended identification key to all 30 species in the Gambarelloides group of *Synalpheus* recorded from the western Atlantic, which incorporates seven new species.

## Introduction

The genus *Synalpheus* Bate, 1888 includes probably more than 150 species of tropical and subtropical shrimp (Chace 1988, Ríos, pers. obs.); they are particularly abundant components of coral reefs and are frequently involved in symbiotic or parasitic relationships (Bruce 1976, Felder and Chaney 1979, Reed *et al.*, Erdman and Blake 1987, Duffy 2003).

Coral reefs are ecosystems supporting high species diversity (Roberts *et al.* 2002, Reaka-Kudla 1997). Strategically located in the middle of the Belizean Barrier Reef, the Smithsonian Institution Marine Field Station at Carrie Bow Cay, Belize provides an excellent opportunity to study the natural history of that biodiversity hotspot (Rützler and Macintyre 1982, Roberts *et al.* 2002, Gibson and Carter 2003). It is not serendipitous that most of the western Atlantic species of *Synalpheus* can be found there at Carrie Bow Cay. The continuous operation of the Marine Field Station since the early 1970s has greatly facilitated scientific expeditions in the area. Nevertheless, among the Crustacea, few groups have been studied extensively: Isopoda (Kenseley 1982, 1984), Mysidacea (Modlin 1987), myodocopid ostracods (Cohen 1989), and parasitic copepods (Cressey 1991).

The Laboratory of Professor Emmett Duffy at the Virginia Institute of Marine Science temporarily houses a large series of *Synalpheus*. Out of the most conservative tally of 40 western Atlantic species, only 2 or 3 are not represented therein; and it includes material from North Carolina, Florida Keys, Bahamas, Panama, and primarily from Carrie Bow Cay, Belize. The collection of sponge-dwelling *Synalpheus*, in particular, has been going on for almost 15 years now. The wealth of ecological and biological information associated with every sample provides added value to the number of species held; indeed, by collecting sponges predominantly using SCUBA, it has been possible to record details on the

microhabitat and biology for most of the shrimp species (Duffy 2003). The most relevant findings include the documentation of eusociality in three species (Duffy 1996a, 1998; Duffy and Macdonald 1999) and the description of three new species (Duffy 1996b, 1998; Ríos and Duffy 1999).

Coutière (1908, 1909) divided the genus *Synalpheus* into six groups of species according to morphological, ecological, and evolutionary features, namely the Comatularum, the Brevicarpus, the Laevimanus (=Gambarelloides), the Neomeris, the Biunguiculatus (=Coutièrei), and the Paulsoni groups. Banner and Banner (1975) reassessed the definitions of the groups, and concluded that only the first three mentioned “may be coherent enough to continue to be recognized”. Species belonging in the Gambarelloides group are morphologically characterized mainly by a brush of thickly packed long setae on the upper surface of the dactyl of the smaller first chela (Coutière 1908, 1909); these setae are distally curved and arranged in transverse parallel rows. Interestingly, the Gambarelloides are known almost exclusively from the Caribbean region, where they constitute the majority of species in the genus *Synalpheus*. Only seven putative Gambarelloides species are known from outside the western Atlantic: *S. parfaiti* from west Africa (Crosnier and Forest 1966); *S. gambarelloides* from the Mediterranean and East Africa, *S. crosnieri*, *S. sladeni*, and *S. spongicola* from East Africa (Banner and Banner 1983); and *S. mulegensis* and *S. occidentalis* from the Gulf of California (Wicksten 1994). In contrast, 30 out of 40 species known from the western Atlantic belong in the Gambarelloides group. It is conceivable that these figures will change when other parts of the world are more carefully surveyed, but for the time being, it appears likely that the Caribbean region is the center of dispersion for the group Gambarelloides.

This chapter is an account of the Gambarelloides group of species of *Synalpheus* from

Carrie Bow Cay, Belize, and it includes an extended diagnosis for each of 11 previously known species, together with preliminary descriptions of six new species. Also included is a complete list of 40 species (Table 2-3) containing ten non-Gambarelloides species, and an identification key (Appendix 1) to all known species in the Gambarelloides group of *Synalpheus* from the western Atlantic. This update incorporates seven previously unknown species, six from Carrie Bow Cay (CBC) plus one from Panama.

Reference material has been deposited in the National Museum of Natural History, Smithsonian Institution in Washington D.C. (USNM). Additional specimens remain at the Virginia Institute of Marine Science (VIMS), Gloucester Point, VA. Measurements correspond to length of carapace (LC) in millimeters, taken from the most posterior edge of the carapace on the dorsal midline to the tip of the rostrum, unless otherwise indicated. Synonymies included are abbreviated.

### Family Alpheidae Rafinesque, 1815

#### Genus *Synalpheus* Bate, 1888

#### Systematic account of selected species in the Gambarelloides group

#### *Synalpheus agelas* Pequegnat and Heard, 1979

##### Plate II

*Synalpheus agelas* Pequegnat and Heard, 1979:110, fig. 1-4; Dardeau 1984:12, Figs. 3-6.

**TYPE MATERIAL-** Holotype male (USNM 171424), 4.6 mm (rostrum excluded), West Flower Garden Bank, Gulf of Mexico, 25 m deep. Allotype ovigerous female (USNM 171425), 4.6 mm (rostrum excluded), Florida Middle Ground, Gulf of Mexico, 30-34 m deep (Pequegnat and Heard 1979).

**MATERIAL EXAMINED-** Three females (at least one ovigerous), 3.8, 3.9, & 4.3 mm

(VIMS 93CBC7501); five males, 3.2-3.8 mm (VIMS 93CBC7502), Carrie Bow Cay, Belize 5 April 1993, living inside *Agelas clathrodes*, 20 m deep. One male, 4.8 mm; one ovigerous female, missing the carapace, but slightly larger than the male (VIMS 90CBC0101), NE of Carrie Bow Cay, Belize 26 April 2001, living inside *Agelas dispar*, 17 m deep. One ovigerous female, 4.9 mm (VIMS 90CBC2902), Carrie Bow Cay, Belize 11 December 1990, living inside *Agelas dispar*, 6 m deep.

**DIAGNOSIS-** Body form subcylindrical; carapace smooth, sparsely setose, with pterygostomian corner produced into bluntly acute angle, and posterior margin with cardiac notch distinct. Rostrum clearly narrower than, and falling slightly short of, orbital teeth. Orbitorostral process absent. Ocular hoods dorsally convex; in dorsal view, bluntly acute, separated from rostrum by deep adrostral sinus. Ocular process, broad. Ocellary beak in lateral view, broad at base, not rod-like. Stylocerite with mesial margin slightly concave and lateral margin strongly convex; tip acute, not sharp; distinctly falling short of distal margin of first segment of antennular peduncle; latter segment without ventromesial tooth, and with 2 basal ventral processes. Basicerite with dorso-lateral corner, forming right angle; longer ventrolateral spine clearly overreaching distal margin of first segment of antennular peduncle. Scaphocerite blade reduced, acute lateral spine robust, with lateral margin slightly concave, almost reaching distal margin of second segment of antennular peduncle; mesial projection at base of scaphocerite present. Third maxilliped with distal circlet of spines on distal segment and without ventrodistal spine on antepenultimate segment.

Major first pereopod massive, fingers shorter than half length of palm; pollex reduced, much shorter than dactyl; in ventral view, outer face of pollex without any protuberance. Palm of chela with distal superior margin produced into prominent bluntly

acute tubercle, downwardly oriented. Merus, extensor margin strongly convex, with distal flat, angular projection.

Minor first pereiopod with palm less than 2 times longer than high; fingers shorter than palm; dactyl with opposing margin straight, blade-like, with short accessory distinct subdistal teeth, perpendicular to dactyl axis; with conspicuous transverse dorsal setal combs on dactyl; pollex with opposing margin straight, blade-like, and subdistal accessory cant. Merus, extensor margin convex, ending in obtuse angle.

Second pereiopod with carpus 4-segmented, shorter than merus.

Third pereiopod dactyl biunguiculate, with flexor unguis thicker than extensor; merus rather thick, usually less than 3.5 times longer than wide, without movable spines on flexor margin; mesial lamella on coxa present. Fourth and 5<sup>th</sup> pereiopods, normal.

First pleura of male with lower edge strongly sinuous, and posterior corner distinctly produced ventrally and anteriorly into thick hook; remaining pleura of male broadly obtuse. First pleopod of male, with about 3 terminal setae on endopod; second pleopod of male with marginal setae on exopod originating close to base; appendix interna on second to fifth male pleopods, present. Telson with space between distal spines greater than one-third of distal margin; marginal convex lobe present; posterior corners adjacent to spines acute, projections not longer than wide. Anal flaps, perianal setae, and postanal setal brush absent. Uropods with 1, seldom 2, fixed tooth on outer margin of exopod, distinctly removed from slightly longer mobile one, latter contiguous to internal fixed tooth.

**COLOR-** Live specimens have a red-orange general appearance, with a brighter orange in the major chela. The black stomach is also prominent in freshly collected specimens.

**VARIATIONS-** In some specimens the rostrum is lanceolate rather than triangular. Sometimes the merus of the third pereopod is elongated, almost four times longer than wide. The most frequent number of lateral fixed teeth on the uropodal exopod is one, but sometimes there are two.

**ECOLOGY-** As expressly indicated by its name, *Synalpheus agelas* was described on the basis of specimens living inside an orange sponge identified by Pequegnat and Heard (1979) as "*Agelas dispar*". At Carrie Bow Cay, we have collected this shrimp both in *A. dispar*, which is brown (Zea 1987) rather than orange, and also in the truly orange *A. clathrodes*.

**DISTRIBUTION-** Western Atlantic: Northern Gulf of Mexico; Florida; Bahamas; Puerto Rico; Belize.

### *Synalpheus androsi* Coutière, 1909

#### Plate III

*Synalpheus androsi* Coutière, 1909: 82, fig. 50; Dardeau 1984:18.

**TYPE MATERIAL-** Holotype female (USNM 38409). Andros Island, Bahamas.

**MATERIAL EXAMINED-** Male, 2.1 mm (VIMS 93CBC4004), outer ridge of Carrie Bow Cay, Belize 24 March 1993 inside sponge *Pseudoceratina crassa*, 13 m deep. Male, 3.2 mm (VIMS 93CBC5201), ovigerous female, 3.5 mm (VIMS 93CBC5202), outer ridge of Carrie Bow Cay, Belize 27 March 1993 inside sponge *Hyatella intestinalis*, 14 m deep. Female, 4.0 mm (VIMS 99CBC3801), ovigerous female, 3.8 mm (VIMS 99CBC3802), male, 3.6 mm (VIMS 99CBC3803), vicinity of Carrie Bow Cay, Belize (16°48'N, 88°05'W), 7 December 1999 inside sponge *Hyatella intestinalis*, 14 m deep. Ovigerous female, 4.6 mm (VIMS 03CBC0501), male, 4.0 mm (VIMS 03CBC0502), outer ridge of Carrie Bow Cay, Belize 17

April 2003 inside sponge *Hyatella intestinalis*, 15 m deep.

**DIAGNOSIS-** Body form subcylindrical; carapace smooth, glabrous, with pterygostomian corner produced into bluntly acute angle, and posterior margin with cardiac notch distinct. Frontal region somewhat protruding over first segment of antennular peduncle, beyond commissure of stylocerite. Rostrum triangular, tip beveled, about as wide as orbital teeth, but slightly longer, and distally upturned. Orbitorostral process absent. Ocular hoods dorsally convex; in dorsal view, bluntly acute, separated from rostrum by deep adrostral sinus. Ocular process nipple-shaped in lateral view, flanged posteriorly under eye. Ocellary beak in lateral view, kidney-shaped. Stylocerite stocky; mesial margin slightly concave, outer strongly convex; tip acute, not sharp; falling short of distal margin of first antennular peduncle; this latter segment without ventromesial tooth, and with 2 basal ventral processes. Basicerite with obtuse dorsolateral corner, and long ventrolateral spine clearly overreaching midlength of second segment of antennular peduncle. Scaphocerite blade absent; acute lateral spine robust, with lateral margin slightly concave, usually overreaching antennular peduncle; mesial projection at base of scaphocerite present. Third maxilliped with distal circlet of spines on distal segment and without ventrodiscal spine on antepenultimate segment.

Major first pereiopod massive, with ovoid profile; fingers shorter than half length of palm; pollex shorter than dactyl; in ventral view, outer face of pollex without any conspicuous protuberance. Palm of chela with distal superior margin produced into prominent bluntly acute tubercle. Merus, extensor margin convex, with flat distal angular projection.

Minor first pereiopod with palm less than two times longer than high; fingers shorter



than palm; dactyl with opposing margin straight, blade-like, with obtuse emargination at midlength, and microscopic subdistal accessory cant parallel to dactyl axis; transverse dorsal setal combs on dactyl, very conspicuous; pollex with opposing surface obliquely concave, and strongly convex keel behind apex. Carpus with conspicuous flange on interior margin. Extensor margin of merus almost straight, ending in obtuse angle.

Second pereopod with carpus 5-segmented, about as long as merus.

Third pereopod *sui generis*, dactyl biunguiculate, with flexor unguis thicker than extensor; propodus with distinct internal surface, concave because of longitudinal crest on posterior edge; carpus with stronger crest on posterior edge and conspicuous longitudinal ridge on anterior edge; merus with crest and ridge on distal half, matching those on carpus; mesial lamella on coxa present. Pereopods 4 and 5 not modified.

First pleura of male with posterior corner acutely produced ventrally; second to fifth pleura of male broadly rounded to obtuse. First pleopod of male with 3 terminal setae on endopod; second pleopod of male with marginal setae on exopod originating near midpoint; appendix interna present on second to fifth male pleopods. Telson, space between distal spines greater than one-third of distal margin; marginal convex lobe present; posterior corners adjacent to spines acute, projections not longer than wide. Anal flaps, perianal setae, and postanal setal brush, absent. Uropods with single fixed tooth on outer margin of exopod, slightly offset from longer mobile spine, adjacent to internal tooth; diaeresis well developed across whole blade.

**COLOR-** Live specimens are transparent with a hue of violet most apparent on the edges of the abdomen. The edges on the distal portion of the major chela are translucent brown-green. The digestive gland and the ovaries are orange-brown. The mature embryos

are brown, more intensely towards the center.

**ECOLOGY-** *Synalpheus androsi* lives in heterosexual pairs, almost exclusively inside the sponge *Hyatella intestinalis*; however, on a couple of occasions we have collected single males inside *Pseudoceratina crassa*, *Hymeniacidon caerulea*, and probably also *Agelas clathrodes*. The latter record is uncertain because sometimes the samples include more than one species of sponge. The eggs are large, fewer than 10 (Plate III) filling the entire brood chamber of large ovigerous females. Consequently, the hatching larva is large, and exhibits the following suite of characters: eyes not covered by carapace; antennule with three distinct segments and two flagella; antenna with fully developed blade on scaphocerite. First pair of pereiopods with chelae present; minor one, without the specialized comb of setae on dorsal surface. First to fourth pereiopods with exopod. Pleopods biramous.

**DISTRIBUTION-** Western Atlantic: Andros Island, Bahamas, and Carrie Bow Cay, Belize.

**REMARKS-** This species is remarkable because of the unique structure of both carpus and merus of the third pereiopod. It was previously known only from the single female holotype, collected at Andros Island, Bahamas (Armstrong 1949). In a male specimen, there is a mobile spine in the cavity of the merus on the third pereiopod. The description of the holotype (Coutière 1909) mentions additional spines on the carpus, besides the typical distal one, which is present in our specimens, but these latter do not have additional spines, only thick setae.

*Synalpheus brevifrons* Chace, 1972

Figure 2-1, Plate III

*Synalpheus brevifrons* Chace, 1972: 89, Figs. 31-32; Dardeau 1984: 26.

**TYPE MATERIAL-** Holotype female (USNM 135371), 2.8 mm (rostrum excluded), Dominica, shallow water.

**MATERIAL EXAMINED-** Male, 3.2 mm (VIMS 95CBC3501), outer ridge of Carrie Bow Cay, Belize 2 July 1995 inside gray sponge lining internal canals of yellow morph of *Pseudoceratina crassa*, 15 m deep. Ovigerous female, 2.9 mm (VIMS 02CBC3602), male, 2.6 mm (VIMS 02CBC3603), The Pinnacles (Sand Bores), Belize, 28 June 2002 inside purple-gray sponge, 1 m deep. Ovigerous female, 3.0 mm (VIMS 03CBC2608), male, 2.9 mm (VIMS 03CBC2609), The Pinnacles (Sand Bores), Belize, 21 April 2003, no host recorded, 1 m deep.

**DIAGNOSIS-** Body form subcylindrical; carapace smooth, with pterygostomian corner produced into bluntly acute angle, and posterior margin with cardiac notch distinct. Rostrum triangular, not upturned, with shallow ventral keel at base; about as long as orbital teeth, but narrower. Orbitorostral process absent. Ocular hoods dorsally convex; in dorsal view, obtuse, margins convex, separated from rostrum by shallow adrostral sinus. Ocular process, broadly obtuse. Ocellary beak in lateral view not rod-like. Stylocerite slender; mesial margin straight; tip acute; clearly not reaching as far as distal margin of first segment of antennular peduncle; this latter segment without mesio-ventral tooth, and with 2 basal ventral processes. Basicerite with dorso-lateral corner obtuse, and with longer ventrolateral spine clearly overreaching distal margin of first segment of antennular peduncle. Scaphocerite blade absent, acute lateral spine robust, with lateral margin slightly concave,

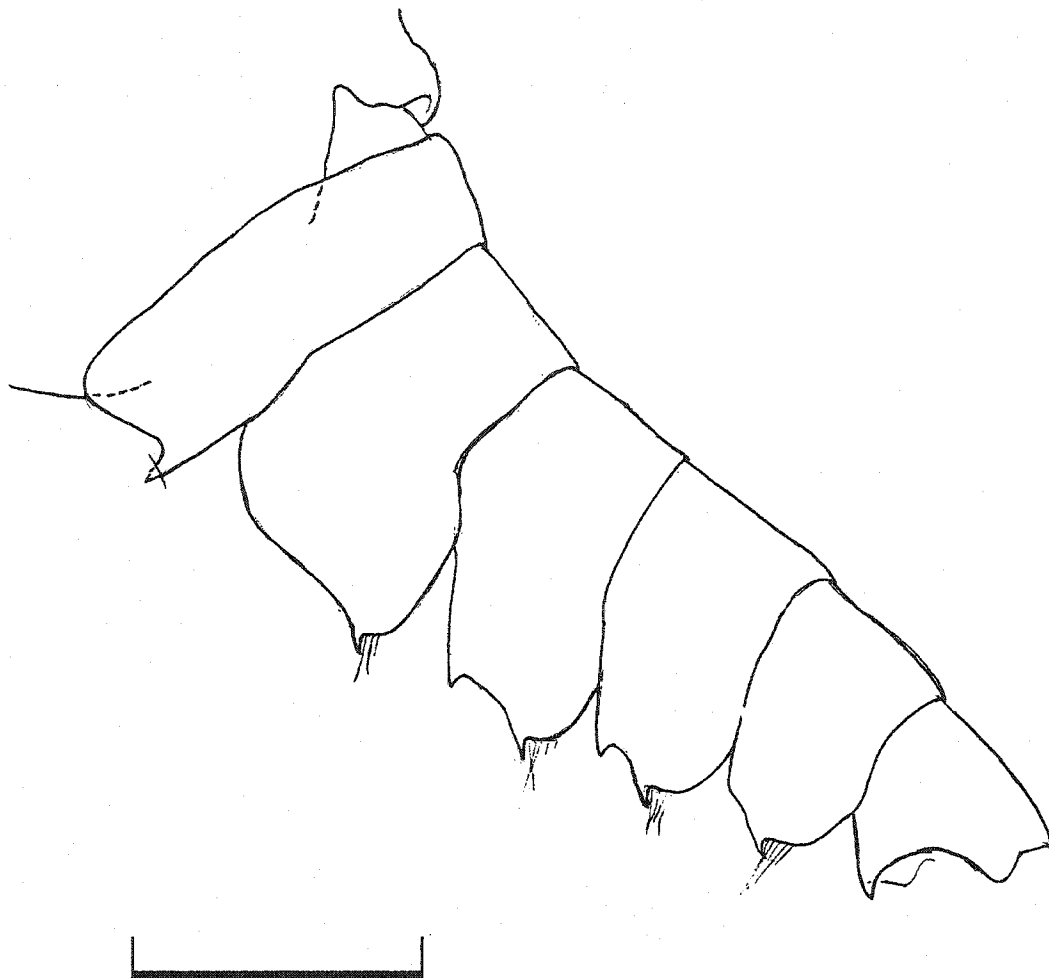


Figure 2-1. *Synalpheus brevifrons* Chace. Male 3.2 mm(VIMS 95CBC3501): lateral view of abdomen. Scale bar = 1mm.

clearly overreaching antennular peduncle; mesial projection at base of scaphocerite present. Carpocerite overreaching tip of scaphocerite. Third maxilliped with distal circlet of spines on distal segment and without ventrodiscal spine on antepenultimate segment.

Major first pereiopod massive, fingers shorter than half length of palm; pollex about as long as dactyl; in ventral view, outer face of pollex without any protuberance. Palm of chela with distal superior margin produced into prominent blunt tubercle. Merus, extensor margin strongly convex, ending in obtuse angle.

Minor first pereiopod with palm clearly less than 2 times longer than high; fingers clearly shorter than palm; dactyl with opposing margin straight, blade-like, with 2 strong subequal distal teeth, parallel to dactyl axis; transverse dorsal setal combs on dactyl, conspicuous, but not dense; pollex with opposing margin straight, blade-like, and 2 strong subequal teeth, parallel to dactyl axis. Extensor margin of merus convex, ending in obtuse angle.

Second pereiopod with carpus 5-segmented, longer than merus.

Third pereiopod slender; dactyl biunguiculate, with subequal ungues; merus without movable spines on flexor margin; mesial lamella on coxa present. Pereiopods 4 and 5 normal.

Male abdomen distinctly flattened. First pleura of male with posterior corner distinctly produced ventrally and anteriorly into a hook; second pleura with posterior corner sharply acuminate ventrally and posteriorly; third and fourth pleura each with two posteriorly oriented hooks; fifth and sixth with single hook also posteriorly oriented. First pleopod of male with 2 or 3 terminal setae on endopod; second pleopod of male with marginal setae on exopod originating near midpoint; appendix interna on second to fifth male pleopods,

present. Telson, space between distal spines greater than one-third of distal margin; marginal convex lobe present; posterior corners adjacent to spines obtuse; mesial pair of spines distinctly subsided and distally upturned. Anal flaps, perianal setae, and postanal setal brush, absent. Uropods with a single fixed tooth on outer margin of exopod, distinctly removed from much longer mobile spine adjacent to internal fixed tooth.

**COLOR-** Live specimens are translucent to milky white with traces of bright gold on the distal edges of the chelae; the digestive gland is faint yellow; the ovaries and the embryos are bright green.

**ECOLOGY-** *Synalpheus brevifrons* lives inside the canals of a filmy gray sponge that grows lining the internal canals of a different sponge, *Pseudoceratina crassa*.

**DISTRIBUTION-** Western Atlantic: Dominica, Belize, possibly also Panama.

**REMARKS-** This species was previously known only from the female holotype; in the original figures by Chace (1972), the antennule appears thicker than in the specimens from Belize. The hooks on the ventral margin of the male abdominal pleura are a striking character, unique among the western Atlantic species of *Synalpheus*; one male had 2 hooks on one of the second pleurae. An ovigerous female from San Blas Islands, Panama, is very similar to *S. brevifrons*, but has a small blade on the scaphocerite and the spines on the dorsal surface of the telson are distinctly removed from the edge. Because this specimen came from a pink unidentified sponge, it seems likely that this is yet another undescribed species.

*Synalpheus chacei* Duffy, 1998

## Plate II

*Synalpheus chacei* Duffy, 1998:389, Figs. 1-5 (and synonymy)

**TYPE MATERIAL-** Holotype male (USNM 282773), 2.4 mm Carrie Bow Cay, Belize, inside *Agelas dispar*, 3 m deep.

**MATERIAL EXAMINED-** Female (?), 2.4 mm (VIMS 96CBC1805), 27 males 1.7-2.4 mm (VIMS 96CBC1806), spur and groove of Carrie Bow Cay, Belize 14 June 1996 inside sponge *Agelas dispar*, 4 m deep.

**DIAGNOSIS-** Body form subcylindrical; carapace smooth, sparsely setose, with pterygostomian corner very obtusely angular, and posterior margin with cardiac notch distinct. Rostrum triangular, about as long, but narrower than orbital teeth, and slightly upturned tip. Orbitorostral process absent, but convex keel present under rostrum base. Ocular hoods dorsally convex; in dorsal view, bluntly triangular, separated from rostrum by deep adrostral sinus. Ocular process broad and shallow. Ocellary beak, triangular in lateral view. Stylocerite stocky; mesial margin slightly concave, occasionally convex; tip blunt; barely reaching midpoint of first segment of antennular peduncle; this latter segment without mesio-ventral tooth, and with 2 basal ventral processes. Basicerite with dorso-lateral corner, straight and with longer ventrolateral spine surpassing midpoint of second segment of antennular peduncle. Scaphocerite blade absent, acute lateral spine robust, with lateral margin slightly concave, overreaching distal margin of second segment of antennular peduncle; mesial projection at base of scaphocerite present. Third maxilliped with distal circlet of spines on distal segment and without ventrodiscal spine on antepenultimate segment.

Major first pereiopod massive, fingers shorter than half length of palm; pollex about as long as dactyl; in ventral view, outer face of pollex without any protuberance. Palm of chela with distal superior margin normally produced into prominent blunt tubercle; merus, extensor margin strongly convex, ending in obtuse angle.

Minor first pereiopod with palm less than 2 times longer than high; fingers shorter than palm; dactyl with opposing margin straight, blade-like, with 2 strong distal teeth, subequal in length, and parallel to dactyl axis; transverse dorsal setal combs on dactyl, very conspicuous, arranged in 2 longitudinal sets separated by a furrow; pollex with opposing margin straight, blade-like, and with 2 strong teeth subequal in length; extensor margin of merus slightly convex, ending in a right angle.

Second pereiopod with carpus 5-segmented, about as long as merus.

Third pereiopod slender; dactyl biunguiculate, with flexor unguis slightly thicker and more straight than extensor; merus without movable spines on flexor margin; mesial lamella on coxa present. Pereiopods 4 and 5 normal.

First pleura of male with posterior corner acutely produced ventrally into wide hook; second pleura of male broadly rounded, occasionally with posterior corner obtuse. Remaining pleura increasingly acute, but not acuminate. First pleopod of male with 3 or 4 terminal setae on endopod; second pleopod of male with marginal setae on exopod originating near midpoint; appendix interna present on second to fifth male pleopods. Telson, space between distal spines about one-third of distal margin; marginal convex lobe present; posterior corners adjacent to spines obtuse. Anal flaps, perianal setae, and postanal setal brush absent. Uropods with a single fixed tooth on outer margin of exopod distinctly removed from thicker and longer mobile spine adjacent to smaller internal fixed tooth.



**COLOR-** Live specimens of *Synalpheus chacei* are translucent in general with a milky wash on the major chela and body; legs and tail fan somewhat transparent; the distal edges in both of the first pair of chelae have a gold to brownish tinge. Sometimes, several red chromatophores are apparent on the carapace between the eyes. The eggs are yellowish to creamy opaque.

**ECOLOGY-** Like *S. regalis* and *S. filidigitus*, *S. chacei* is also eusocial and is consistently found in aggregations of several tens usually with a single reproductive female (Duffy 1998). This species dwells in the internal canals of several species of sponges, including *Agelas dispar*, *A. clathrodes*, *Niphates amorpha*, and *Lissodendoryx colombiensis* in Panama, and *Agelas dispar*, *A. clathrodes*, *Hyatella intestinalis*, *Hymeniacidon amphilecta*, and *Lissodendoryx strongylata* in Belize.

**DISTRIBUTION-** Western Atlantic: Carrie Bow Cay, Belize; San Blas Islands, Panama; British Virgin Islands.

### *Synalpheus* sp. 1, new species

Figures 2-2 through 2-5, Plate I

**TYPE SPECIMENS-** Holotype male, 8.5 mm (USNM 1019038), allotype ovigerous female, 9.9 mm (USNM 1019039), Twin Cays, Belize 26 April 2001 from canals of sponge *Lissodendoryx colombiensis*, 1 m deep. Paratypes: male, 7.6 mm, female, 9.2 mm (USNM 1019040); male, 7.6 mm, ovigerous female 9.1 mm (USNM 1019041) Twin Cays, Belize 2 December 1999 from canals of sponge *Lissodendoryx colombiensis*, 2 m deep.

**DESCRIPTION OF HOLOTYPE-** Body form subcylindrical; carapace smooth, glabrous, with pterygostomial corner produced into bluntly acute angle, and posterior

margin with cardiac notch distinct. Rostrum lanceolate, distally upturned, slightly longer, but clearly narrower than orbital teeth. Orbitorostral process absent. Ocular hoods dorsally convex; in dorsal view, hoof-shaped, laterally convex, mesially concave, separated from rostrum by deep adrostral sinus. Ocular process produced into elongated fingerlike structure. Ocellary beak with superior margin straight and inferior strongly convex. Stylocerite slender; tip acute; mesial margin convex; distinctly shorter than distal margin of first segment of antennular peduncle; this latter segment without ventromesial tooth, and with 2 basal ventral processes. Basicerite without spine on dorsolateral corner, and with longer ventrolateral spine clearly overreaching tip of stylocerite. Scaphocerite blade reduced, acute lateral spine robust, with lateral margin slightly concave, not overreaching antennular peduncle, slightly surpassing basicerite lateral spine; mesial corner at base of scaphocerite, right-angled. Carpocerite overreaching antennular peduncle. Third maxilliped with distal cirlet of spines on distal segment and without ventrodiscal spine on antepenultimate segment. Remaining mouthparts as figured.

Major first pereopod massive, fingers about half length of palm; pollex shorter than dactyl; in ventral view, outer face of pollex with an obtuse basal protuberance. Palm of chela with distal superior margin produced into prominent tubercle overhanging an acute spine. Merus, extensor margin strongly convex, with distal flat angular projection on mesial face.

Minor first pereopod with palm more than twice as long as high; fingers clearly shorter than palm; dactyl with opposing surface straight, with 2 strong distal teeth, subequal in length, and parallel to dactyl axis; transverse dorsal setal combs on dactyl, very conspicuous; pollex with opposing surface straight, ending in one strong tooth and one slightly shorter, subdistal tooth. Extensor margin of merus slightly convex, ending in obtuse

angle.

Second pereopod with carpus 5-segmented, distinctly longer than merus.

Third pereopod, dactyl biunguiculate, with flexor unguis clearly thicker than extensor; propodus with a row of 11 (right leg) or 10 (left leg) mobile spines on lower margin, and 2 paired subdistal spines; carpus slightly longer than half the propodus, with strong mobile spine on distal flexor corner; merus longer than twice carpus length, about 4 times longer than wide, without movable spines on flexor margin; ischium subtrapezoidal, shorter than carpus, devoid of spines; basis shorter than ischium, lower margin strongly convex; coxa with mesial lamella. Fourth pereopod similar to third, but weaker. Fifth pereopod similar to third, but more slender, propodus with 11 transverse parallel rows of thick setae on posterior face, and 5 (right leg) or 4 (left leg) mobile spines on ventral margin; carpus almost  $3/4$  as long as propodus, without distal spine; merus about as long as propodus, without spines.

First abdominal pleura of male, anterior corner almost a right angle, posterior corner distinctly produced ventrally and anteriorly, hook-like; second to fifth pleura of male produced ventrally into acute angle; sixth abdominal segment with acute projection on posteroventral corner, shallow inferior concavity, acutely produced triangular lateral lobe, shallow obtuse upper emargination, and convex dorsal margin slightly overhanging telson. Female allotype with first abdominal pleura with inferior margin slightly concave, second to fourth broadly rounded, fifth acutely produced ventrally. First pleopod of male, with 6 terminal setae on endopod; second pleopod of male with marginal setae on exopod originating close to base. Appendix interna on second to fifth pleopods, present in both sexes. Telson, space between distal spines about one-third of distal margin; marginal convex

lobe present; posterior corners adjacent to spines rectangular. Anal flaps present. Perianal setae absent. Postanal setal brush present. Right uropod, with 5 fixed teeth on outer margin of exopod; mobile spine distinctly removed from lateral fixed teeth, but contiguous to subequally long wider fixed tooth on mesial side, diarsis well defined; left uropod similar, but with 4 fixed teeth and supernumerary mobile spine.

**COLOR-** Live specimens were uniformly brilliant orange with darker tips on the major chela; the walking legs and the tail fan were more translucent; the digestive gland was olive green.

**ETYMOLOGY-** The specific name for this species will be in honor of Michael R. Dardeau, Dauphin Island Sea Lab, Alabama, in recognition of his work on *Synalpheus* from the Gulf of Mexico.

**ECOLOGY-** This unnamed species of *Synalpheus* is most frequently found living inside the orange sponge *Lissodendoryx colombiensis*. It also inhabits the loggerhead sponge *Spherospongia vesparium* and on rare occasions it has been collected inside a couple of unidentified sponges. An infested sponge usually houses a few heterosexual pairs along with other species of *Synalpheus*.

**DISTRIBUTION-** North Carolina, Belize.

**REMARKS-** This species belongs in a group of closely related and morphologically similar species which includes *S. longicarpus* and *S. pandionis* (Table 2-1). The combination of hoof-shaped ocular hoods, strong dorsal spines on the telson, strong teeth on the minor chela, and a well defined cardiac notch on the carapace provide the most useful characters in identifying *Synalpheus* sp. 1. Like *S. longicarpus*, *Synalpheus* sp.1 reaches the largest sizes among the *Synalpheus* from the western Atlantic.

Figure 2-2. *Synalpheus* sp. 1, new species. Paratype female 9.1 mm (USNM 1019041): a, anterior region of carapace and cephalic appendages, dorsal view; b, same, lateral view. Paratype male 7.6 mm (USNM 1019040): c, abdomen, lateral view. Paratype ovigerous female 9.2 mm (USNM 1019040): d, abdomen, lateral view. Allotype ovigerous female 9.9 mm (USNM 1019039): e, abdomen, lateral view. Paratype male 8.2 mm (VIMS 01CBC7408): f, detail of 4th-6th abdominal pleurae, lateral view. Scale bar = 1 mm for a, b; 2 mm for c, d; 2.5 mm for e; and 1.2 mm for f.

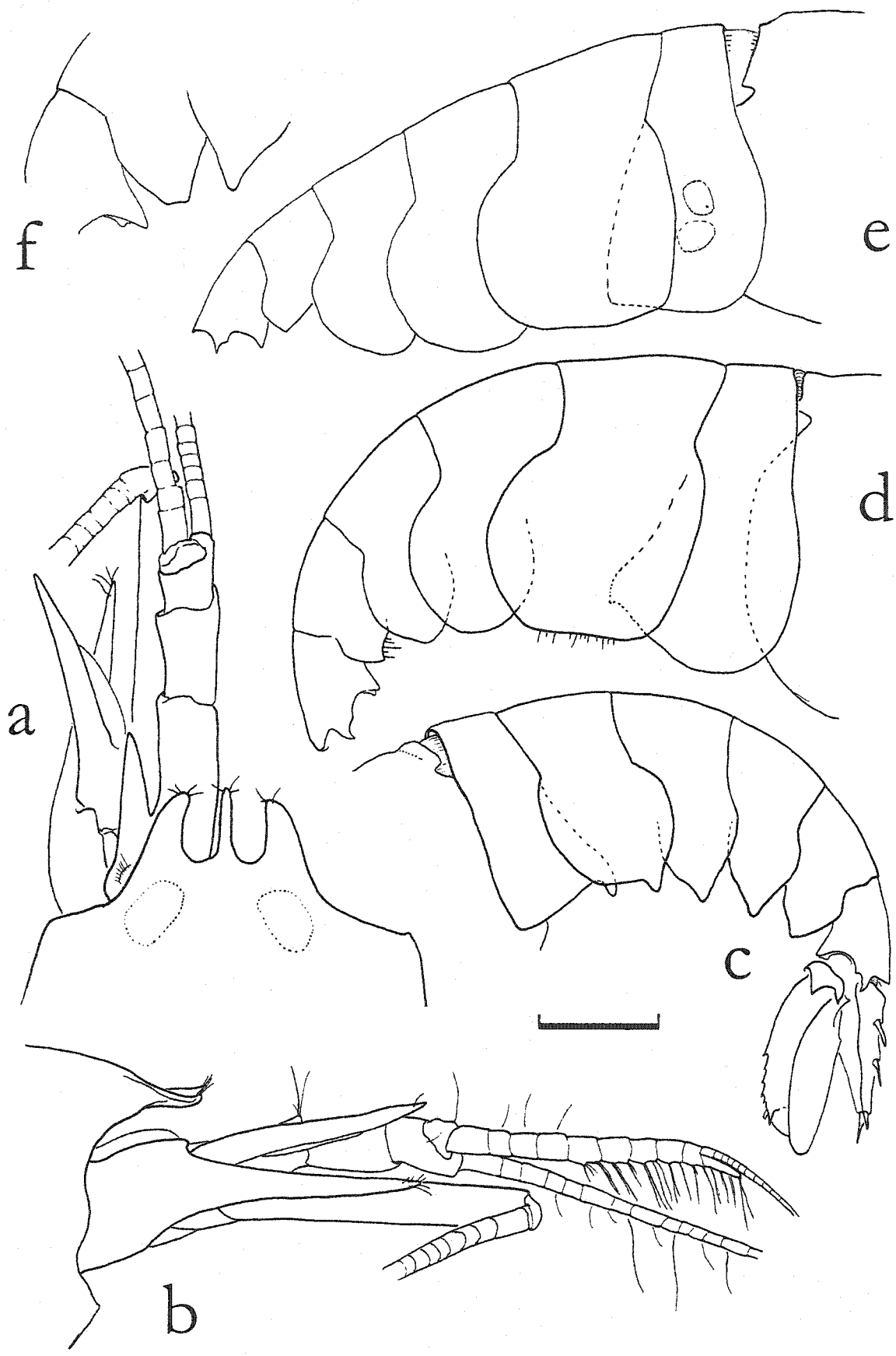


Figure 2-3. *Synalpheus* sp. 1, new species. Paratype male 7.6 mm (USNM 1019040): a, major first pereopod, lateral view; b, same, tip of pollex, ventral view; c, same, merus, lateral view; d, minor first pereopod, lateral view; e, distal portion of same, alternate lateral view. Paratype ovigerous female 9.2 mm (USNM 1019040): f, distal portion of chela of major first pereopod, lateral view. Paratype female 9.1 mm (USNM 1019041): g, distal portion of chela of major first pereopod, lateral view; h, telson and uropods, dorsal view. Scale bar = 1 mm for a, c, g; 0.66 mm for b; 0.5 mm for d, f, h; and 0.12 mm for e.

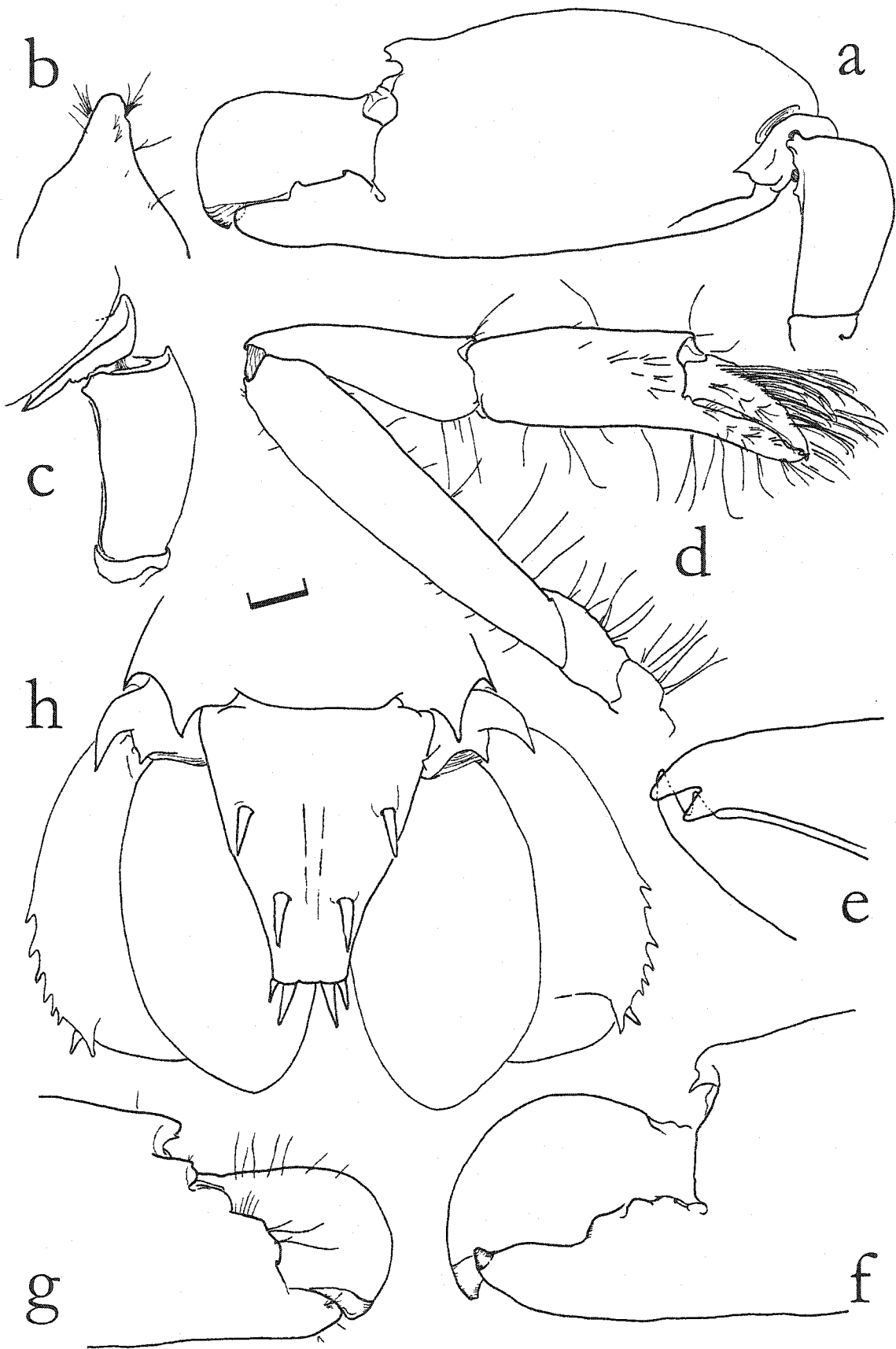




Figure 2-4. *Synalpheus* sp. 1, new species. Paratype male 7.6 mm (USNM 1019040): a, left third pereiopod; b, same, detail of distal portion; c, left fourth pereiopod; d, same, detail of distal portion; e, left fifth pereiopod; f, same, detail of distal portion; g, left second pereiopod; h, same, detail of distal portion. Scale bar = 1 mm for a, c, e, g; 0.25 mm for b, d, f; and 0.5 mm for h.

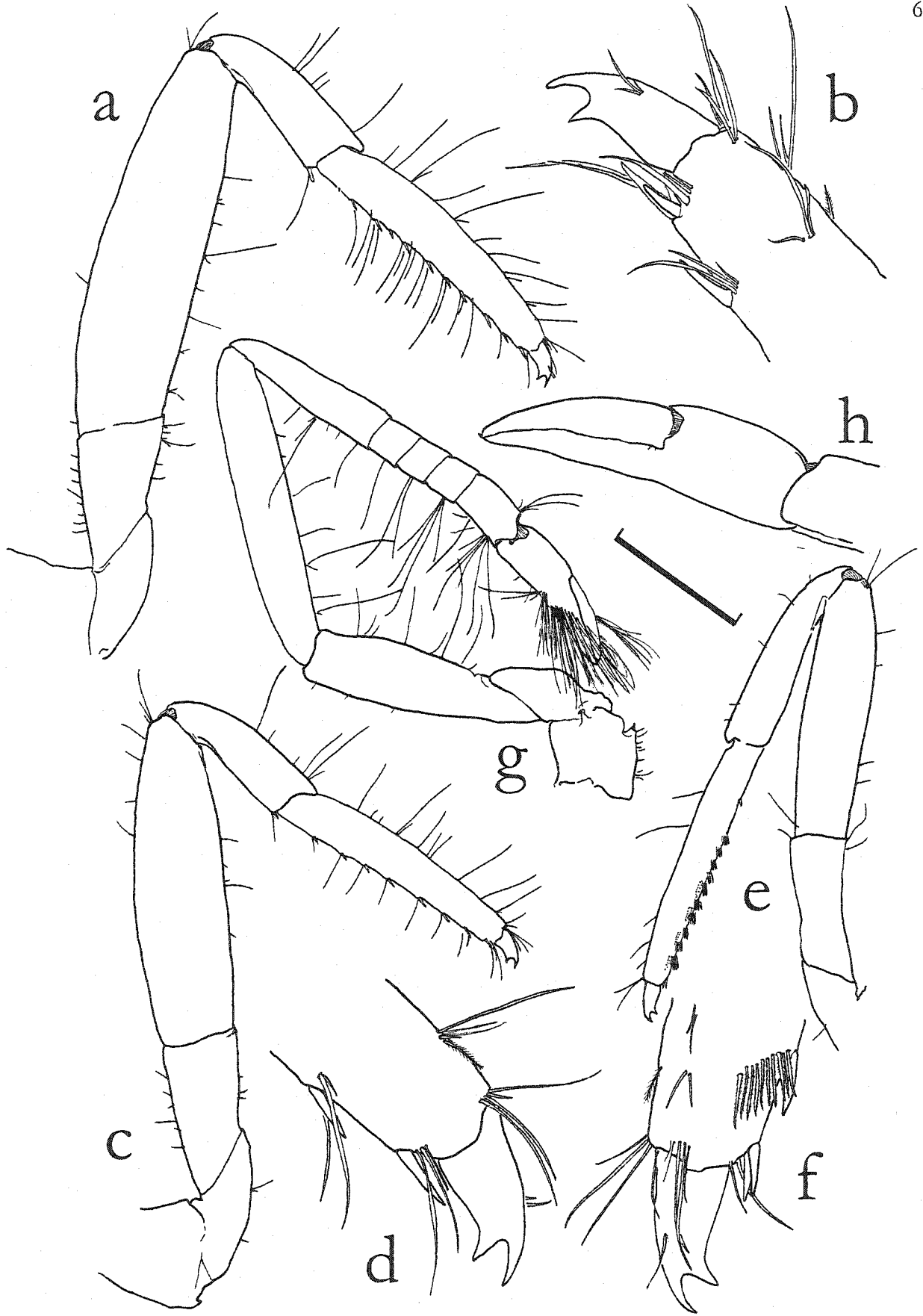
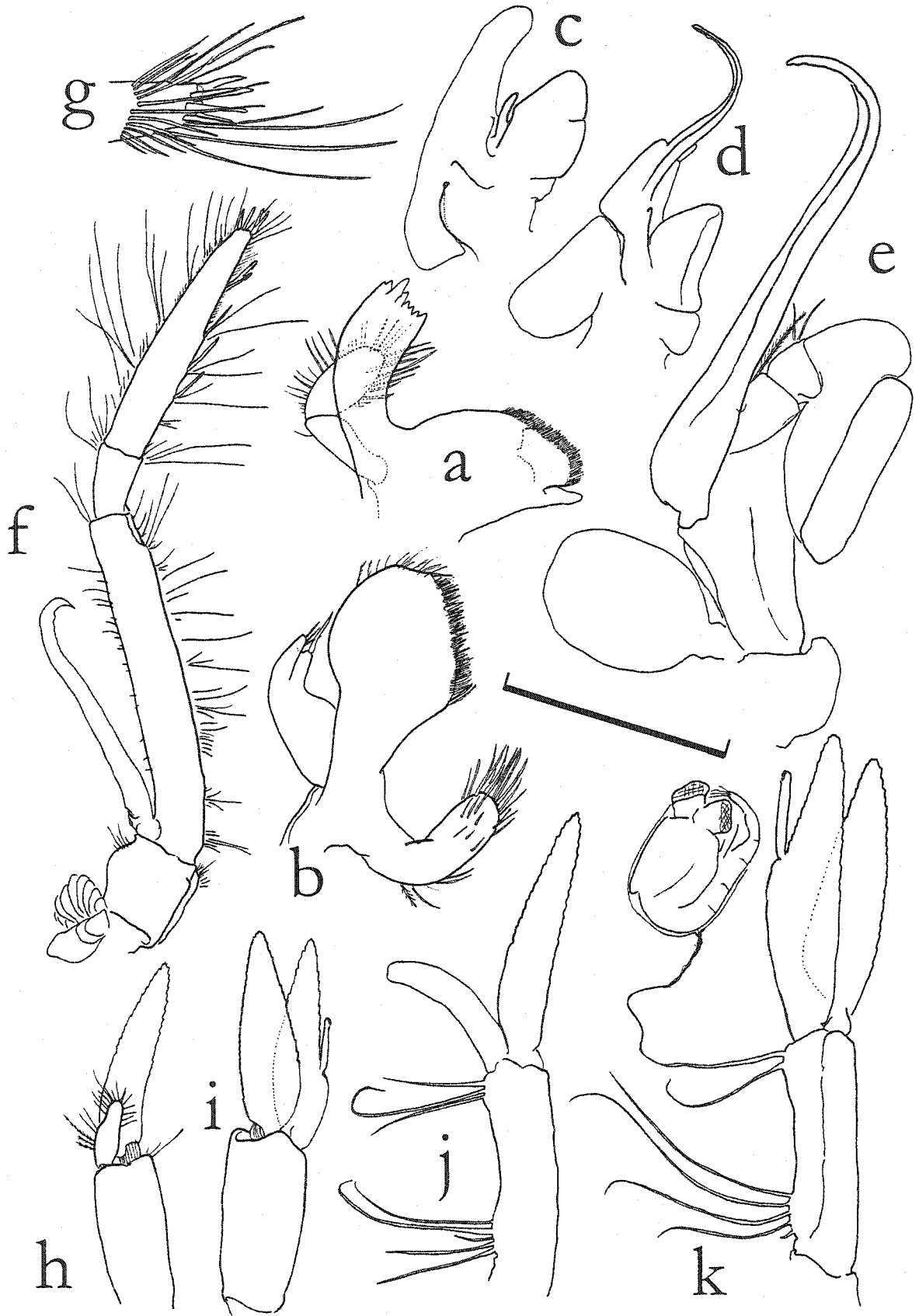


Figure 2-5. *Synalpheus* sp. 1, new species. Paratype male 7.6 mm (USNM 1019040): a, right mandible; b, right first maxilla; c, right second maxilla; d, right first maxilliped; e, right second maxilliped; f, right third maxilliped; g, same, detail of tip; h, left first pleopod; i, left second pleopod. Paratype ovigerous female 9.2 mm (USNM 1019040): j, first pleopod; k, left second pleopod with egg. Scale bar = 1 mm for a, b, e, g; and 2 mm for c, d, f, h, i, j, k.



## *Synalpheus* sp. 2, new species

Figures 2-6 through 2-9, Plate III

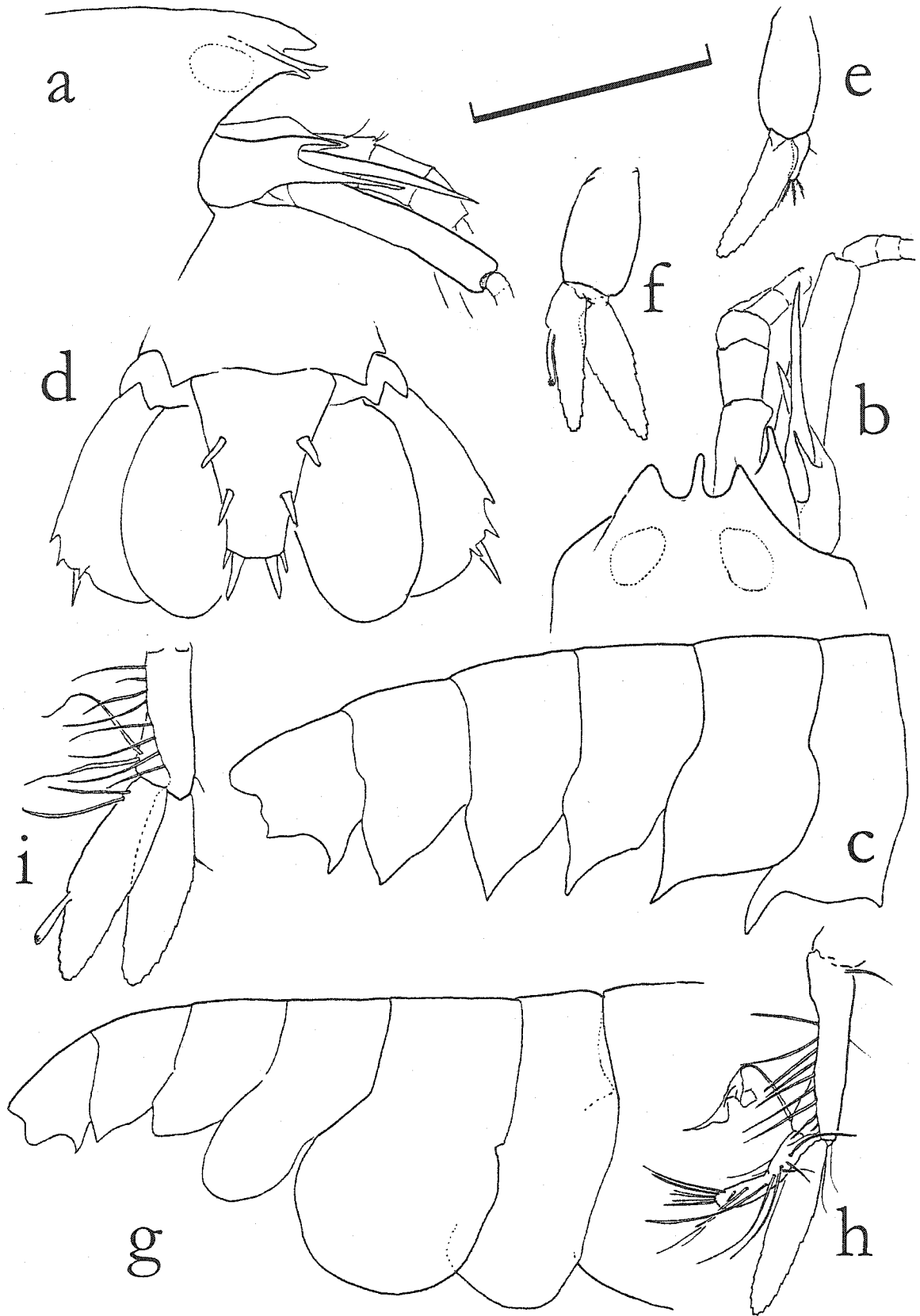
"*Synalpheus rathbunae* A" Duffy 1996c: *passim* (in part).

**TYPE SPECIMENS-** Holotype male, 3.0 mm (USNM 1019042), allotype ovigerous female, 3.6 mm (USNM 1019043), The Pinnacles (Sand Bores), SW of Carrie Bow Cay Belize 2 May 2001 inside the canals of a midnight blue sponge *Hymeniacidon caerulea*, 2 m deep. Paratypes: male, 2.7 mm (USNM 1019044), male, 2.9 mm (USNM 1019045), from same sponge specimen as holotype; male, 3.1 mm (USNM 1019046), South end of ridge (16°48'N, 88°05'W) Carrie Bow Cay, Belize, 6 Dec 1999 in bright orange sponge *Lissodendoryx* sp., 18 m deep.

**DESCRIPTION OF HOLOTYPE-** Body form subcylindrical; carapace smooth, sparsely setose, with pterygostomian corner produced into broad acute angle, and posterior margin with cardiac notch distinct.

Rostrum lanceolate, about as long, but clearly narrower than orbital teeth, and distally upturned. Ventral surface of carapace behind rostrum, flat. Ocular hoods dorsally convex; in dorsal view, broad, bluntly triangular, margins slightly convex, separated from rostrum by deep adrostral sinus; hoods meeting smoothly under base of rostrum. Ocular process like a swollen thick surface. Ocellary beak in lateral view rod-like. Stylocerite thick; mesial margin slightly concave; tip acute; distinctly shorter than distal margin of first segment of antennular peduncle; this latter segment without ventromesial tooth, and with 2 basal ventral processes. Basicerite with strong sharp spine on dorsal margin, reaching about as far as tip of stylocerite, and with longer ventrolateral spine almost reaching distal margin of second segment of antennular peduncle. Scaphocerite blade absent, acute lateral spine robust, with lateral margin straight,

Figure 2-6. *Synalpheus* sp. 2, new species. Holotype male 3.0 mm (USNM 1019042): a, anterior region of carapace and cephalic appendages, lateral view; b, same, dorsal view; c, abdomen, lateral view. Paratype male 2.9 mm (USNM 1019045): d, telson and uropods, dorsal view. Paratype male 2.7 mm (USNM 1019044): e, first pleopod; f, second pleopod. Allotype ovigerous female 3.6 mm (USNM 1019043): g, abdomen, lateral view; h, first pleopod; i, second pleopod. Scale bar = 1 mm for a, b, c, d; 1.1 mm for e, f, h, i; and 1.5 mm for g.



clearly overreaching antennular peduncle, but not reaching as far as distal margin of carpocerite; mesial corner at base of scaphocerite, obtuse. Third maxilliped with distal circllet of spines on distal segment and without ventrodistal spine on antepenultimate segment.

Major first pereiopod massive, somewhat inflated proximally, fingers clearly not longer than half length of palm; pollex reduced, clearly shorter than dactyl; in ventral view, outer face of pollex with an obtuse basal protuberance. Palm of chela with distal superior margin produced into prominent tubercle with acute inwardly directed spine. Merus, extensor margin strongly convex, with distal angular projection.

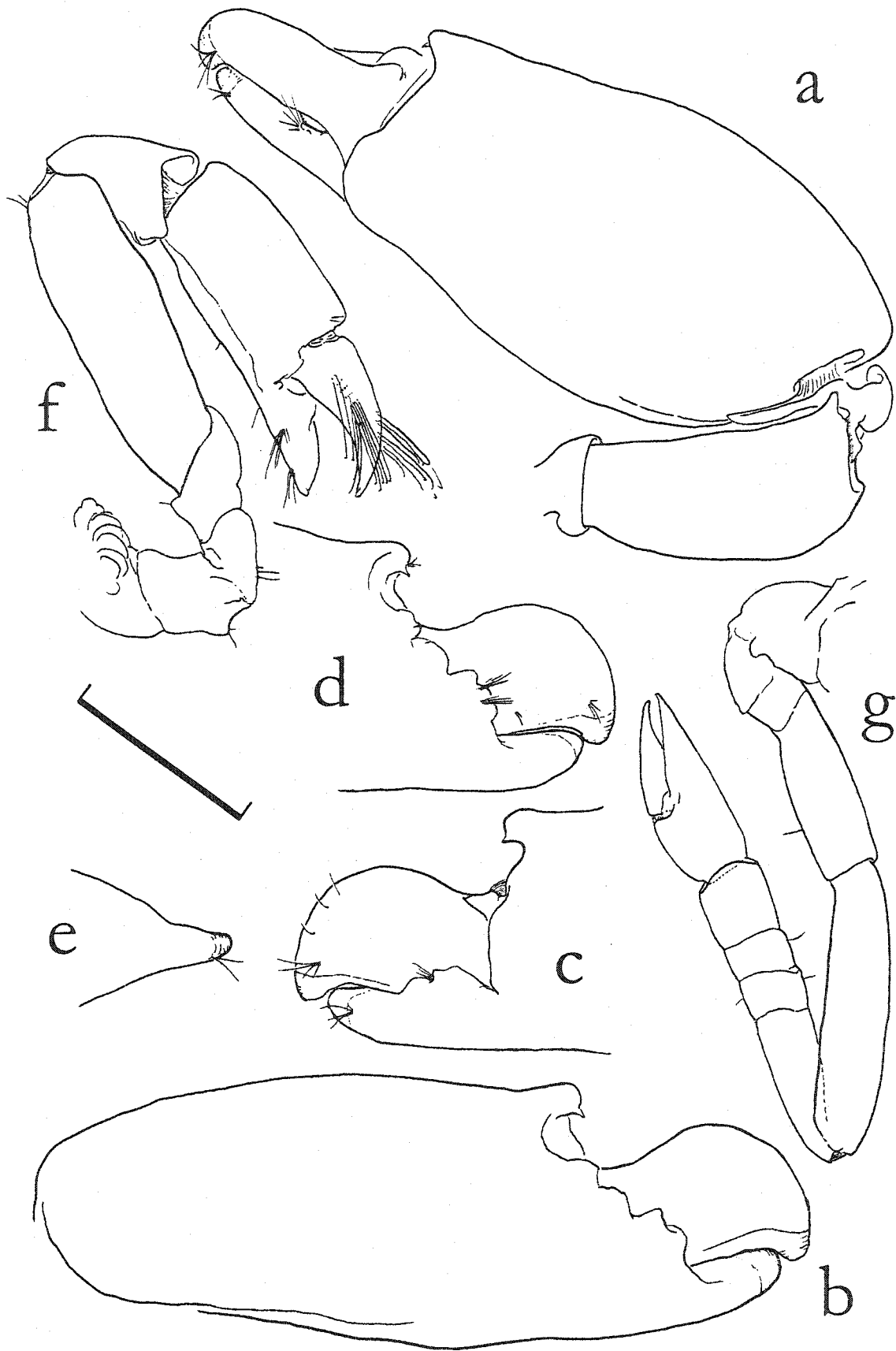
Minor first pereiopod with palm less than 2 times longer than high; fingers unquestionably shorter than palm; dactyl with opposing surface obliquely concave, with no hint of second tooth; transverse dorsal setal combs on dactyl, very conspicuous, arranged in two distinct sets, the mesial one shorter; pollex with opposing surface obliquely concave, and no hint of second tooth. Extensor margin of merus convex, ending in obtuse angle.

Second pereiopod with carpus 4-segmented, about as long as merus.

Third pereiopod slender; dactyl biunguiculate, with flexor unguis clearly thicker than extensor; propodus with a row of 5 mobile spines on the lower margin, and two paired subdistal spines; carpus about half as long as propodus, with a delicate mobile spine on distal flexor corner; merus longer than propodus, slightly longer than 3 times as wide, without movable spines on flexor margin; ischium subtrapezoidal, about as long as carpus, devoid of spines; basis shorter than ischium, lower margin strongly convex; coxa with mesial lamella, present. Fourth and fifth pereiopods similar to third, but fifth with 4 transverse rows of setae on flexor margin of propodus, and carpus without distal spine.



Figure 2-7. *Synalpheus* sp. 2, new species. Paratype male 2.7 mm (USNM 1019044): a, major first pereiopod, dorsal view; b, same, lateral view; c, same, distal portion, lateral view; d, same, alternate view; e, same, tip of pollex, ventral view; f, minor first pereiopod, lateral view; g, right second pereiopod. Scale bar = 1 mm for a, b, c, d, e; and 0.7 mm for f, g.



First pleura of male with posterior corner strongly produced ventrally into tooth with posterior margin convex, anterior corner slightly produced into acute angle; second to fifth pleura of male produced into acute angle ventrally. First pleopod of male, with 3 or 4 terminal setae on endopod; second pleopod of male with marginal setae on exopod originating near midpoint; appendix interna on second to fifth male pleopods, present. Telson, space between distal spines equal to one-third of distal margin, and without convex lobe; posterior corners adjacent to spines obtuse. Anal flaps absent. Perianal setae absent. Postanal setal brush absent. Uropods with 2 fixed teeth on outer margin of right exopod and one on left; robust mobile spine distinctly removed inwards, and submesial fixed tooth slightly superimposed on mobile spine; both of these abnormally duplicated on right exopod.

**COLOR-** Live specimens have a general translucent gold-orange hue with sparse chromatophores; the fingers and distal margin of palm of major chela are more intense orange. Digestive gland is olive-green to brown.

**FIRST LARVA-** Eight hatchling larvae were obtained in the laboratory from a wild-caught ovigerous female. These first larvae are crawling megalopae similar to the one described from *S. brooksi* (Dobkin 1965). They have the front of the carapace trispinose, covering the eyes; both pairs of chelae are functional and not dimorphic; the carpus of the second pair has 3 segments; the pleopods and the uropods are both biramous. The first larva of *S. sp. 2* differs from that of *S. brooksi* in the following details: the fingers of the first pair of chelae are simple, not bifid; the telson has only one pair of spines on the distal margin; the scaphocerite is more slender, without any suggestion of a blade.

**ETYMOLOGY-** It will be an honor to name this species after Dr. Elizabeth Canuel, Virginia Institute of Marine Science, in appreciation not only of her assistance with our early

field research on *Synalpheus*, but also because of her unconditional support while studying such a fascinating shrimp.

**VARIATIONS-** The number of fixed teeth on the exterior margin of the uropodal exopod is most frequently 2, occasionally 1 or 3, with rare records of 4 and 5 only in one of the uropods, most probably resulting from supernumerary duplications. In a few specimens one or both of the second to fourth pleura have 2 points instead of the normal 1, in almost every one of these instances, again it only happens on just one of the two sides of the abdominal segment. The holotype has a supernumerary pleopodal ramus emerging anteriorly to the first right pleopod, such a peculiar abnormality has not been recorded previously.

**ECOLOGY-** *Synalpheus* sp. 2 inhabits the canals of *Hymeniacidon caerulea* and *Lissodendoryx* spp. with occasional records from other sponges. Its population structure appears variable, ranging from aggregations including several adults of both sexes, through colonies of tens or hundreds of individuals with only one or two breeding females.

**DISTRIBUTION-** San Blas Islands, Panama; Carrie Bow Cay, Belize; Florida Keys, USA.

**REMARKS-** This is a third species in the *S. rathbunae* complex and, aside from the genetic differences already documented (Duffy 1996c), the consistent morphological characters that follow warrant the unequivocal distinction of the three species (Table 2-2). The anterior corner of the first pleura in the males of both *S. sp. 2* and *S. regalis* is clearly produced into an acute angle while it is broadly rounded in *S. rathbunae*. Also, the protuberance dorsally overhanging the base of the dactyl in the major chela lacks the accessory spinule and is distinctly acute and upwardly oriented in *S. rathbunae*, but it has a small spine and is conspicuously blunt in the two other species. Additionally, *S. regalis* differs from *S. sp. 2* by having the abdominal pleura less pointed, a conspicuous fringe of long setae

Figure 2-8. *Synalpheus* sp. 2, new species. Paratype male 2.7 mm (USNM 1019044): a, right third pereopod; b, same, detail of distal portion; c, right fourth pereopod; d, same, detail of distal portion; e, right fifth pereopod; f, same, detail of distal portion. Scale bar = 1 mm for a, c, e; and 0.24 mm for b, d, f.

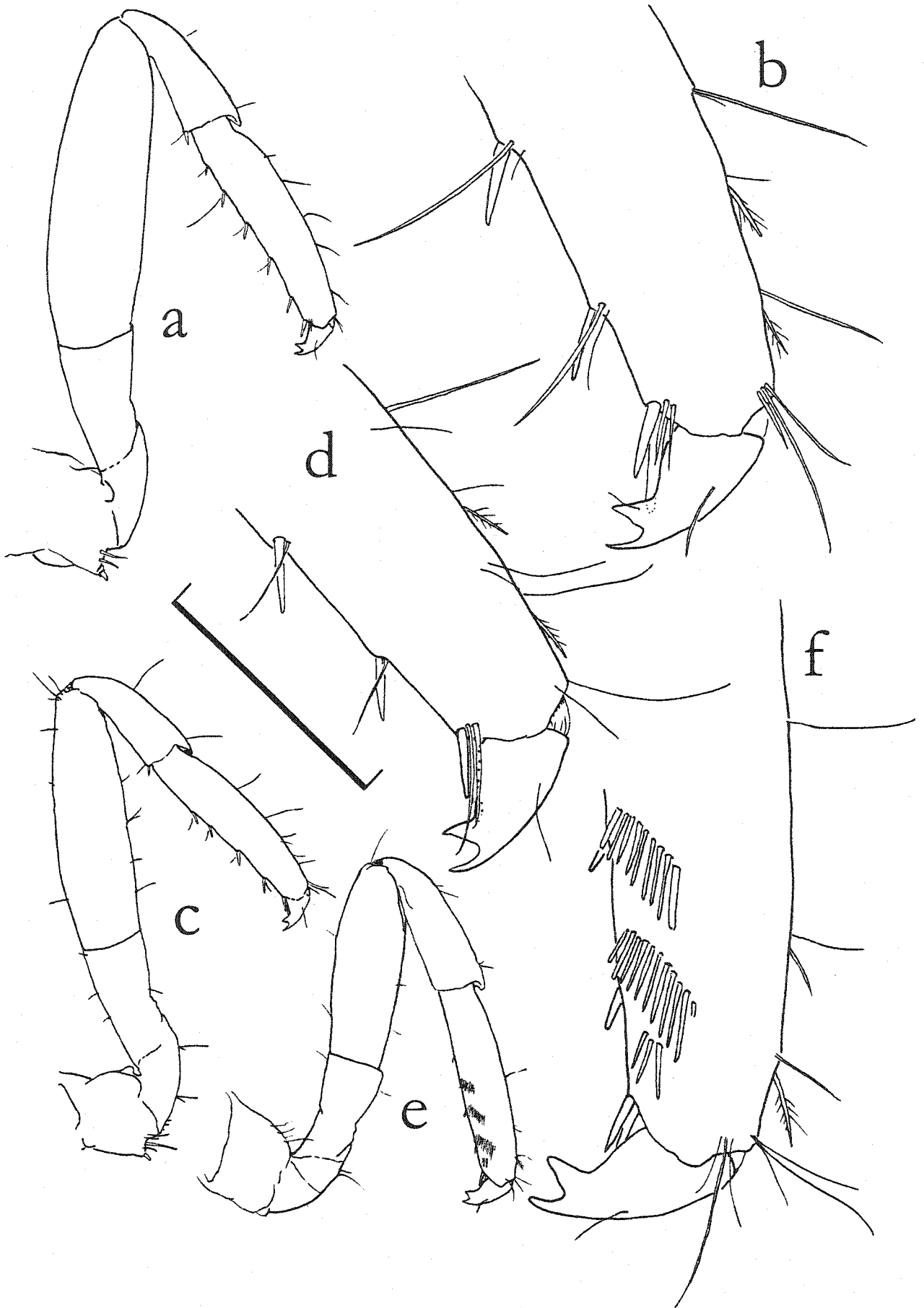
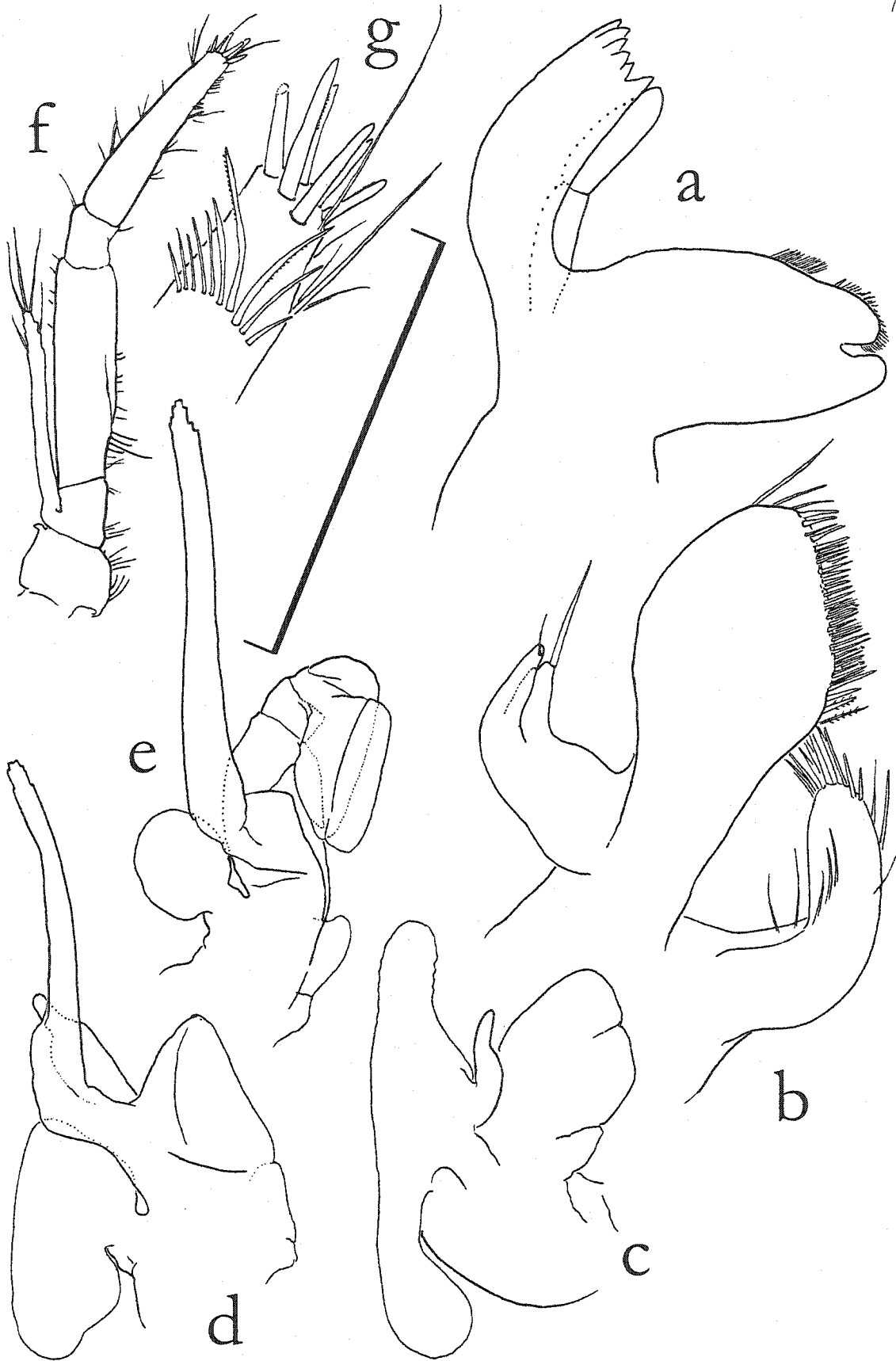


Figure 2-9. *Synalpheus* sp. 2, new species. Mouthparts. Paratype male 2.7 mm (USNM 1019044): a, right mandible; b, right first maxilla; c, right second maxilla; d, right first maxilliped; e, right second maxilliped; f, right third maxilliped; g, same, detail of tip. Scale bar = 1 mm for a, b, g; 2 mm for c, d, e; and 4 mm for f.





on the lower margin of the first abdominal pleura, and more slender fingers on the second chelae. Samples collected from *Lissodendoryx colombiensis* in Panama have a remarkably high incidence of an abdominal parasitic isopod; every specimen appeared to be a partially feminized male, with the abdominal pleura broadly rounded, and an occasional hint of the anterior angle on the first one. The major chela in the Panamian specimens is indistinguishable from that of *S. sp. 2*, but the final identity of these samples remains to be established.

### *Synalpheus filidigitus* Armstrong, 1949

Figures 2-10 and 2-11, Plate II

*Synalpheus filidigitus* Armstrong 1949: 15, fig. 5; Duffy 1996c: *passim*; Duffy and Macdonald 1999: 284.

**TYPE MATERIAL-** Holotype male 2.4 mm (AMNH 9572): Barahona Harbor, República de Santo Domingo, 1932-1933, J. C. Armstrong, coll.

**MATERIAL EXAMINED-** Holotype male 2.4 mm (AMNH 9572): Barahona Harbor, República de Santo Domingo. Five males, 2.3-2.4 mm (USNM 1019061), Curlew Ridge, Belize 27 APR 2001, from a colony of 88 males and a single ovigerous female (2.9 mm), inside a sponge *Xestospongia* sp. growing among dead *Madracis* sp., 15 m deep.

**DIAGNOSIS-** Body form subcylindrical; carapace smooth, glabrous, with pterygostomian corner obtusely angular, and posterior margin with cardiac notch distinct.

Rostrum triangular, clearly narrower than and slightly surpassing orbital teeth; distally upturned and with ventral margin convex. Orbitorostral process absent. Ocular hoods dorsally convex; in dorsal view, broadly triangular, separated from rostrum by deep adrostral

sinus. Ocular processes absent. Ocellary beak in lateral view rod-like. Stylocerite slender; tip acute; reaching about as far as distal margin of first segment of antennular peduncle; this latter segment without ventromesial tooth, and with 2 very small basal ventral processes. Basicerite with sharp spine on dorsal margin not surpassing stylocerite, and with longer ventrolateral spine reaching distal half of second segment of antennular peduncle. Scaphocerite blade absent, acute lateral spine robust, clearly overreaching antennular peduncle; mesial corner at base of scaphocerite, obtuse. Carpocerite slightly surpassing scaphocerite. Third maxilliped with distal circlet of spines on distal segment and without ventrodistal spine on antepenultimate segment

Major first pereiopod massive, fingers clearly not longer than half length of palm; pollex reduced, slightly shorter than dactyl; in ventral view, outer face of pollex without any protuberance. Palm of chela with distal superior margin produced into prominent tubercle with acute spine. Merus, extensor margin strongly convex, ending in obtuse angle, sometimes with a hint of shallow angular projection.

Minor first pereiopod with palm clearly less than 2 times longer than high; fingers about as long as palm; dactyl with opposing surface excavate, with subdistal accessory bump and accessory tooth flanking apex; transverse dorsal setal combs on dactyl, very conspicuous; pollex with opposing surface obliquely concave, and no hint of second tooth. Extensor margin of merus convex, ending in obtuse angle.

Second pereiopod, chela distally tapering, dactyl and pollex with sets of anteriorly directed stiff simple setae on distal-most margins; with carpus 4-segmented, about as long as merus.

Figure 2-10. *Synalpheus filidigitus* Armstrong. Male holotype 2.4 mm (AMNH 9572): a, anterior region of carapace and cephalic appendages, lateral view (right scaphocerite missing); b, same, dorsal view. Male 2.3 mm (USNM 1019061): c, left minor first pereiopod (setal combs on dactyl omitted), lateral view; d, same, tip of dactyl, ventrolateral view; e, same, tip of pollex, lateral view; f, left second pereiopod, lateral view; g, same, tip of chela with some setae removed, lateral view; h, left third pereiopod, lateral view; i, same, detail of distal portion, lateral view. Scale bar = 1.3 mm for a, b, c, f; 1.0 mm for h; and 0.25 mm for d, e, i, g.

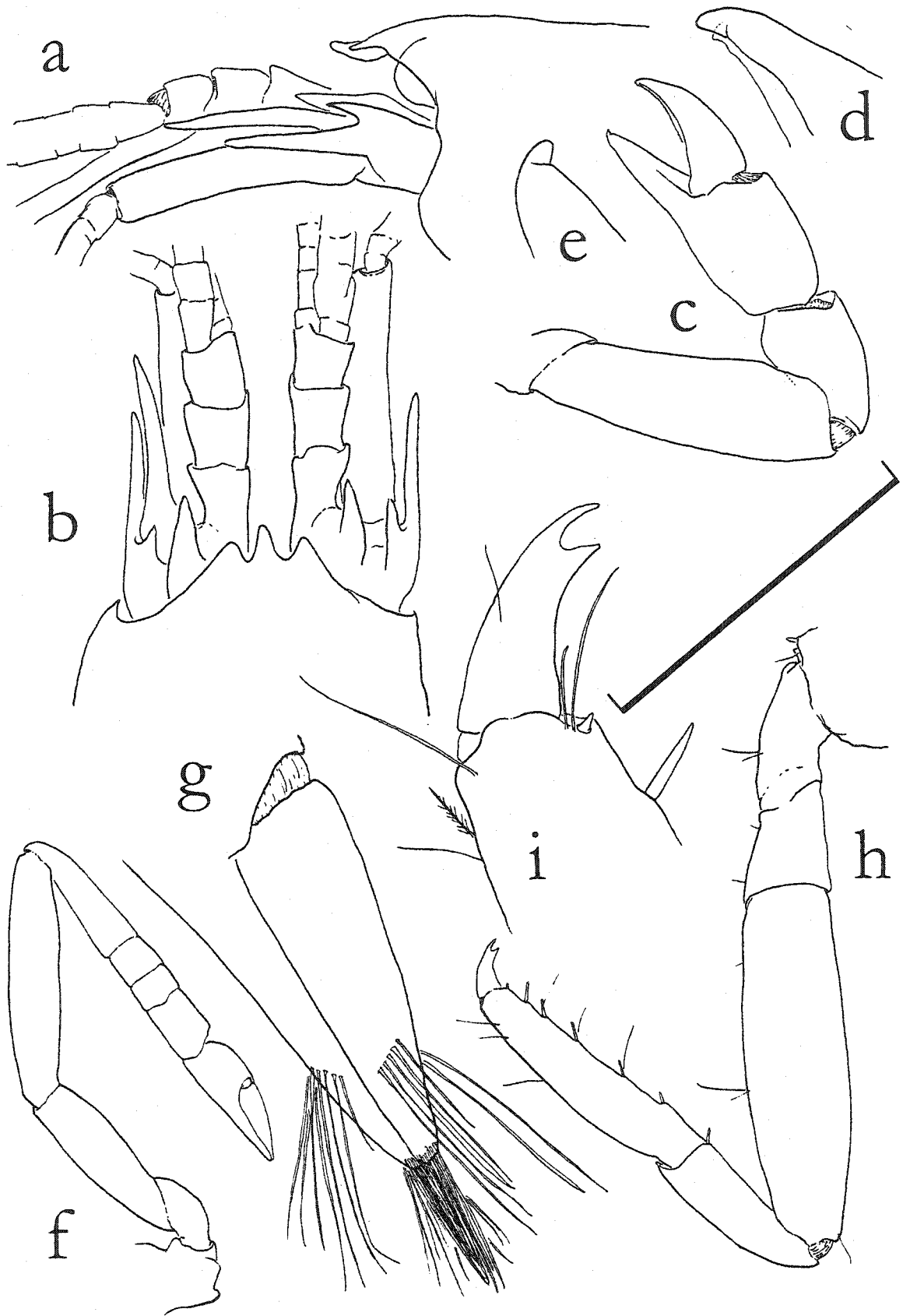
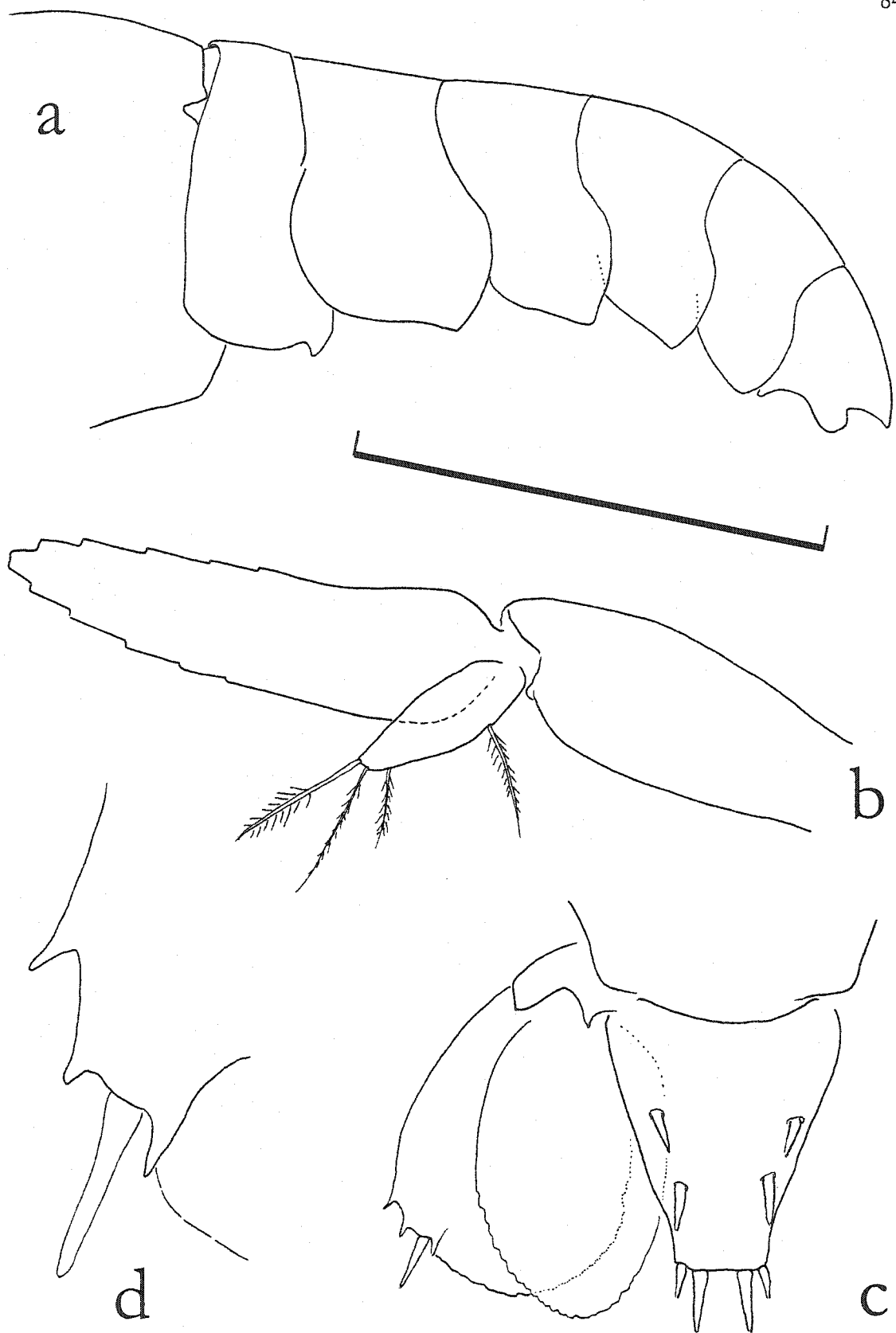


Figure 2-11. *Synalpheus filidigitus*. Male 2.4 mm (USNM 1019061): a, abdomen, lateral view. Incomplete moult (VIMS 01CBC0502): b, first pleopod; c, telson and left uropod, dorsal view; d, distolateral corner of left uropod, dorsal view. Scale bar = 1.6 mm for a; 0.41 mm for b; 1.0 mm for c; and 0.31 mm for d.



Third pereopod slender; dactyl biunguiculate, with flexor unguis thicker than extensor; merus without movable spines on flexor margin; mesial lamella on coxa present.

Pereopods 4 and 5 normal.

First pleura of male with posterior corner produced ventrally into short broadly acute hook; posterior corner of second pleura of male produced into obtuse angle. First pleopod of male, with 3 terminal setae on endopod; second pleopod of male with marginal setae on exopod originating near midpoint; appendix interna on second to fifth male pleopods, present. Telson, space between distal spines about one-third of distal margin; marginal convex lobe absent; posterior corners adjacent to spines obtuse. Anal flaps absent. Perianal setae absent. Postanal setal brush absent. Uropods with 2 fixed teeth on outer margin of exopod; mobile spine slightly over thrice as long as closer adjacent submesial fixed tooth; this latter distinctly receded from anteriormost margin.

**COLOR-** Live specimens have an overall translucent appearance with bright yellow margins on most of the segments of the body and appendages. The ovaries and developing embryos are an intense bright yellow; the digestive gland is a yellowish-salmon color.

**VARIATIONS-** The number of fixed teeth on the lateral margin of the uropodal exopod is almost always 2, with few smaller specimens having only one. Four specimens in the colony examined lack a rostrum, while the queen has an asymmetrical frontal border due to a broadened adrostral sinus on the right side. Two of the specimens (USNM 1019061) lack the protuberance overhanging the base of the dactyl on the major chela, just as Armstrong (1949) recorded in few of his specimens. According to the observations by Duffy and Macdonald (1999), the female in the examined colony is a mature queen; she is

well differentiated from the rest of the members by having a larger body size, broad abdominal pleurae, and two minor chelipeds on the first pereopods.

**ECOLOGY-** *Synalpheus filidigitus* lives inside sponges growing among branches of coral, usually *Madracis mirabilis*. At Carrie Bow Cay it seems to be restricted to the sponges *Xestospongia* spp. and *Oceanapia* sp., with incidental records from a third species, *Hyatella intestinalis*. Like *S. regalis* and *S. chacei*, *S. filidigitus* is also a eusocial species forming colonies with a single reproductive female living with tens of males and juveniles (Duffy and Macdonald 1999).

**DISTRIBUTION-** Western Atlantic: Dominican Republic and Belize.

**REMARKS-** *Synalpheus filidigitus* is closely related to a complex of three species (Duffy 1996c) similar to *S. rathbunae*; all four species have a sharp spine on the dorsal margin of the basicerite, they lack any traces of blade on the scaphocerite, and have only four segments in the carpus of the second chelae. They can be separated by a combination of consistent morphological characters (Table 2-2). When Armstrong (1949) erected *S. filidigitus*, he fully acknowledged the similarity of this species to *S. rathbunae* and listed five characters to distinguish them: length of spine on dorsal margin of basicerite, tubercle overhanging base of major chela dactyl, merus of minor chela, fingers of second chelae, and merus of third pereopod. The name that Armstrong (1949) gave to the species comes from what he called "threadlike" fingers on the chela of the second pair of pereopods; as shown in his figure 5c, this is indeed a most peculiar feature. The examination of several specimens under high magnification suggests that this character might be absent at least occasionally; considering that the tips of the fingers are obscured by the presence of distal and subdistal brushes of



stiff simple setae on both the dactyl and the pollex, additional observations are necessary to verify that those specimens without the filiform tips have not just lost them due to trauma.

In the diagnosis of the species, Dardeau (1984) concurred with Armstrong and described the fingers as filiform, without any further comments; he also recorded the finger of the minor chela as being simple, but in this case again higher magnification of the structure evidences a rather intricate pattern unique among the complex of species related to *S. rathbunae*.

### *Synalpheus goodei* Coutière, 1909

#### Plate IV

*Synalpheus goodei* Coutière, 1909: 58, fig. 33; Dardeau 1984: 40, *pro pars*, fig. 18-21, *nec S. osburni* Schmitt 1933.

? *Synalpheus goodei*: Verrill, 1922: 116, Plates 37-40.

**TYPE MATERIAL-** No holotype designated; there are 59 syntypes (USNM 24821) consisting of 38 males, 20 females (13 ovigerous), and 1 juvenile. Bermudas, G. Brown Good, coll. A lectotype has been designated (Ríos, in prep.).

**MATERIAL EXAMINED-** Two males, 4.5, 5.8 mm (USNM 1019062), Twin Cays, Belize 26 June 1995, inside sponge *Xestospongia wiedenmayeri*, among mangrove roots 1.5 m deep.

**DIAGNOSIS-** Body form subcylindrical; carapace smooth, sparsely setose, with pterygostomian corner produced into bluntly acute angle, and posterior margin with cardiac notch distinct.

Rostrum lanceolate, narrower and longer than orbital teeth, with convex inferior margin prolonged posteriorly beyond anteriormost edge of carapace, and distally upturned.

Ocular hoods dorsally convex; in dorsal view, bluntly acute, separated from rostrum by deep adrostral sinus. Ocular process broad. Ocellary beak in lateral view, thick. Stylocerite stout; mesial margin slightly concave; tip acute; reaching distal-fifth of first segment of antennular peduncle; this latter segment without ventromesial tooth, and with 2 basal ventral processes. Basicerite with acute dorsal margin, and with longer ventrolateral spine reaching distal margin of second segment of antennular peduncle. Scaphocerite blade reduced, robust sharp lateral spine with lateral margin slightly concave, clearly overreaching antennular peduncle; mesial projection at base of scaphocerite present. Carpocerite overreaching scaphocerite. Third maxilliped with distal circlet of spines on distal segment and without ventrodiscal spine on antepenultimate segment.

Major first pereopod massive, fingers slightly longer than half length of palm; pollex slightly shorter than dactyl; in ventral view, outer face of pollex without any protuberance. Palm of chela with distal superior margin produced into prominent tubercle and distal acute spine. Merus, extensor margin strongly convex, with distal flat angular projection.

Minor first pereopod with palm less than 2 times longer than high; fingers unquestionably shorter than palm; dactyl with opposing surface distally excavate, with 2 strong distal teeth, subequal in length, and 1 accessory protuberance, all situated perpendicularly to dactyl axis; transverse dorsal setal combs on dactyl, very conspicuous; pollex with opposing surface obliquely concave, and two subdistal accessory cants. Extensor margin of merus distally convex, ending in obtuse angle.

Second pereopod with carpus 5-segmented, about as long as merus.

Third pereopod stout; dactyl biunguiculate, with flexor unguis thicker than extensor; merus without movable spines on flexor margin; mesial lamella on coxa present.

First pleura of male with posterior corner produced ventrally into shallow triangular hook; second pleura of male with posterior corner obtusely prolonged. First pleopod of male, with about 8 terminal setae on endopod; second pleopod of male with marginal setae on exopod originating close to base; appendix interna on second to fifth male pleopods, present. Telson, space between distal spines about one-third of distal margin; marginal convex lobe, inconspicuous; posterior corners adjacent to spines, rectangular. Anal flaps absent. Perianal setae absent. Postanal setal brush present. Uropods with 5 to 12, usually 7 or 8, fixed teeth on outer margin of exopod, and thick triangular fixed spine slightly overreached by slender mobile spine.

**COLOR-** Live specimens have a general translucent milky white background with sparse pink chromatophores; distal portion of chelae with marginal highlights of greenish gold; tip of major chela, bright orange to brown; ripe ovaries, light gray to brown; digestive gland, olive green. This account does not match what Verrill (1922) recorded in great detail studying specimens from Bermudas. Because the identity of the material from Belize is supported by the examination of the syntypes (also from Bermudas), the specimens analyzed by Verrill may belong in a different species.

**VARIATIONS-** The dorsolateral corner on the basicerite ends usually in a sharp acute angle, but occasionally it is reduced only into a right angle. The blade of the scaphocerite is always narrow and shorter than the adjacent spine, but it can reach the distal margin of any one of the three segments of the antennular peduncle or just half the length of the stylocerite. The blade can also be reduced to a mere convex emargination, but even in such cases the presence of marginal setae remains constant. There seems to be a growth-related pattern to the degree of the development of the hook on the posterior corner on the first

abdominal pleura; in some smaller males there is only a triangular ventrally directed flap. Also, the number of fixed teeth on the lateral margin of uropodal exopods is reduced in smaller specimens.

**ECOLOGY-** *Synalpheus goodei* inhabits the internal canals of living sponges. We have found it both in *Xestospongia wiedenmayeri* growing on mangrove roots and in *Pachypellina podatypa* in shallow reef environments. It forms groups of several individuals with slightly more males than females.

**DISTRIBUTION-** Western Atlantic: Bermudas, Gulf of Mexico, Belize.

**REMARKS-** *Synalpheus goodei* is superficially similar to *S. williamsi*, but they can be easily separated by the differences mentioned under the account for *S. williamsi*.

Dardeau (1984) synonymized *S. osburni* Schmitt, 1933 with this species. However, examination of the holotype (AMNH 3599) of *S. osburni* from Puerto Rico, suggests that it should be considered a valid species. Still the only known specimen, the holotype of *S. osburni* has a most remarkable feature unaccounted for, *i. e.*, a spine on the distal border of the palm of the minor chela. Other differences with *S. goodei* include the strikingly elongated rostrum, the total absence of a blade on the scaphocerite or any traces of setae on the mesial margin of the lateral spine, the protuberance overhanging the spine on the distal margin of the palm of the major chela, and the shape of the dactyl of the smaller chela. Discovery of additional specimens, including males, will undoubtedly provide more characters to distinguish these two species.

### *Synalpheus* sp. 3, new species

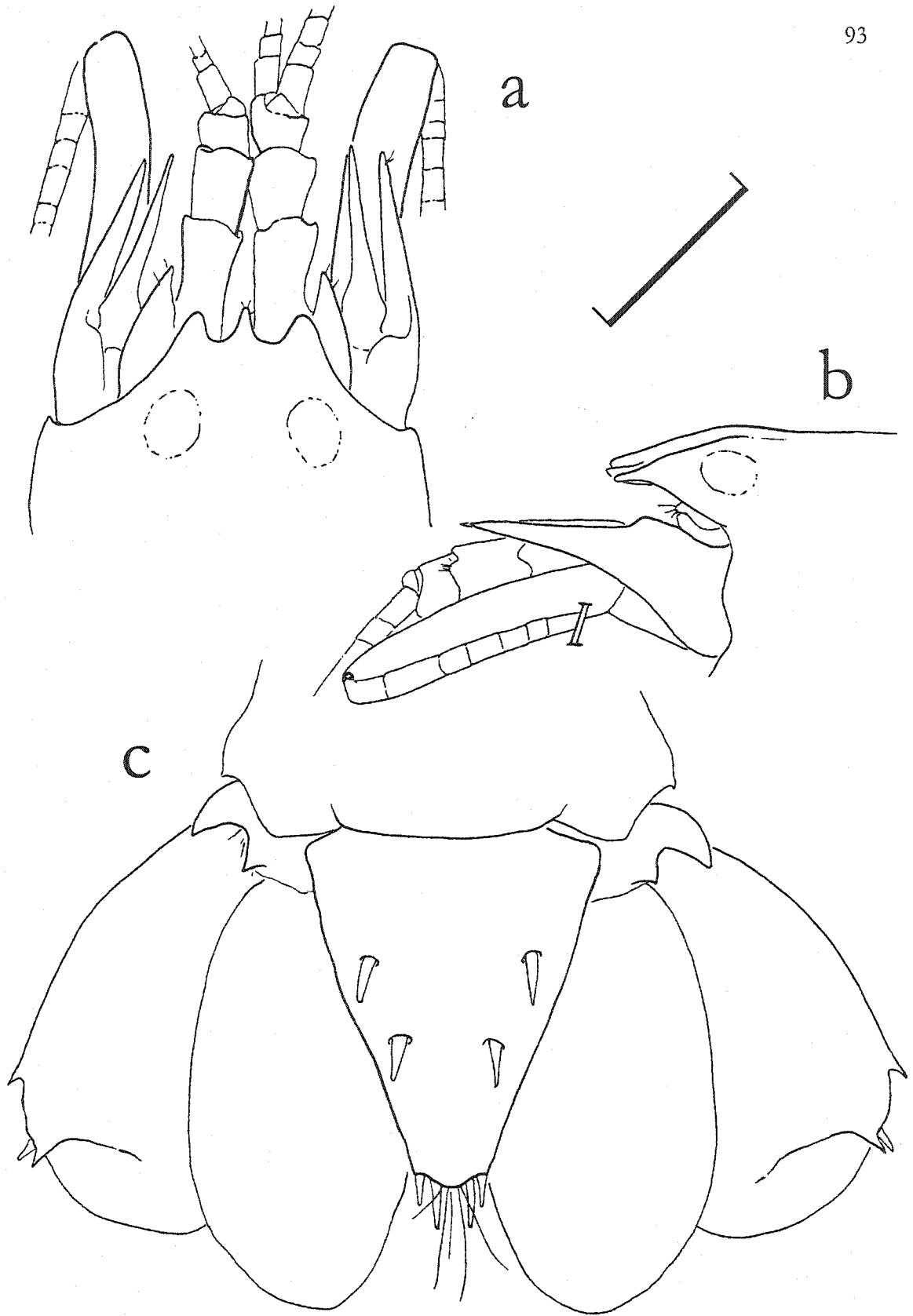
Figures 2-12 through 2-16, Plate II

**TYPE SPECIMENS-** Holotype male, 5.0 mm (USNM 1019047), allotype ovigerous female, 5.1 mm (USNM 1019048), paratypes: two males, 4.3 & 4.7 mm (USNM 1019049) Carrie Bow, Belize, 4 May 2001, from canals of same specimen of sponge *Hymeniacion amphilecta*, 6m deep.

**DESCRIPTION OF HOLOTYPE-** Body form subcylindrical; carapace smooth, sparsely setose, with pterygostomian corner produced into bluntly acute angle, and posterior margin with cardiac notch distinct. Rostrum about as long as orbital teeth, but distinctly narrower, distally upturned; margins in dorsal view, straight. Orbitorostral process absent. Ocular hoods dorsally convex; in dorsal view, bluntly acute, separated from rostrum by deep adrostral sinus. Ocular process triangular, flanged posteriorly onto lower side of eye. Ocellary beak in lateral view not rod-like, broader at base. Stylocerite acute, but tip blunt; mesial margin slightly concave; surpassing midpoint of first; this segment without ventromesial tooth, and with two basal ventral processes. Basicerite without spine on dorsolateral corner, and with longer ventrolateral spine reaching distal half of second segment of antennular peduncle. Scaphocerite blade absent, acute lateral spine robust, with lateral margin slightly concave, slightly surpassing basicerite spine, not overreaching antennular peduncle; mesial projection at base of scaphocerite present. Third maxilliped with distal circlet of spines on distal segment and without ventrodiscal spine on antepenultimate segment. Remaining mouthparts as figured.

Major first pereiopod massive, fingers clearly shorter than half length of palm; pollex slightly shorter than dactyl; in ventral view, outer face of pollex without any marked

Figure 2-12. *Synalpheus* sp. 3, new species. Allotype ovigerous female 5.1 mm (USNM 1019048): a, anterior region of carapace and cephalic appendages, dorsal view; b, same, lateral view; c, telson and uropods, dorsal view. Scale bar = 1 mm for a, b; and 0.76 mm for c.



protuberance. Palm of chela with distal superior margin produced into tapering conical blunt tubercle not conspicuously directed upward; in frontal view, tubercle does not show ventral surface and does not rise above palmar profile. Merus, extensor margin strongly convex, ending in obtuse angle.

Minor first pereiopod with palm clearly less than two times longer than high; fingers clearly shorter than palm; dactyl with opposing margin straight, blade-like, with 2 distinct distal teeth, subequal in length, and parallel to dactyl axis; transverse dorsal setal combs on dactyl, very conspicuous; pollex with opposing margin straight, blade-like, and 2 distinct teeth subequal in length. Extensor margin of merus convex, ending in right angle.

Second pereiopod with carpus 5-segmented, subequal to merus.

Third pereiopod slender; dactyl biunguiculate, with flexor unguis clearly thicker than extensor; propodus with row of 7 mobile spines on flexor margin and one pair of distal mobile spines flanking base of dactylus; carpus with distal mobile spine on flexor margin; merus almost 4 times longer than wide, without movable spines on flexor margin; mesial lamella on coxa present. Fourth pereiopod similar to third, slightly weaker. Fifth pereiopod weaker than fourth; propodus with only 2 spines on flexor margin, and 5 transverse combs of stout setae on ventral face; carpus without distal spine.

First pleura of male with posterior corner distinctly produced ventrally and anteriorly into small hook; second pleura of male broadly rounded; third to fifth pleura of male progressively acute, but not pointed. First pleopod of male, with 6 terminal setae on endopod; second pleopod of male with marginal setae on exopod originating near midpoint; appendix interna on second to fifth male pleopods, present. Telson, space between distal spines about one-third of distal margin; marginal convex lobe present; posterior corners



adjacent to spines obtuse. Anal flaps, perianal setae, and postanal setal brush absent.

Uropods with a single fixed tooth on outer margin of exopod distinctly removed from the mobile one, this latter slightly longer and slender than adjacent inner fixed tooth.

**COLOR-** Live specimens (Plate II) from *Hymeniacion amphilecta* have a general milky translucent appearance with regularly scattered red chromatophores mainly on the carapace and major chela; besides the amber cutting edges on the fingers of the major chela, the margins of the dactylus and the distal border of the palm have a strong hue of orange. Developing eggs and ovaries are both brick-red to brownish-orange. Live specimens from *Lissodendoryx colombiensis* are mostly transparent with scattered contracted chromatophores, and have a light purple hue most apparent in smaller specimens.

**ETYMOLOGY-** The specific name for this species will be a Greek word that means "one's own" or "pertaining to oneself". The name signifies the distinctiveness of this species regardless of its strong resemblance to *S. brooksi* Coutière.

**VARIATION-** In some males, the abdominal pleura posterior to the second one form an acute angle, without prolonging into an acuminate projection. As juveniles have 4 segments in the carpus of the second pereopod, occasionally there are six segments in some larger specimens. The teeth arrangement on the uropodal exopod is constant, except in small juveniles where the external tooth has the appearance of being not fully developed. As previously mentioned, there seems to be some variation in color related to the sponge host.

**ECOLOGY-** This unnamed species of *Synalpheus* lives in groups of up to several tens of specimens with numerous ovigerous females and juveniles present; it inhabits inside the canals of the sponges *Hymeniacion amphilecta* in Belize and *Lissodendoryx colombiensis* in Panama.

Figure 2-13. *Synalpheus* sp. 3, new species. Allotype ovigerous female 5.1 mm (USNM 1019048): a, chela of major first pereiopod in lateral view; b, same, anterior region alternate lateral view; c, same, dorsal view; d, same, tip of pollex, ventral view. Paratype male 4.7 mm (USNM 1019049): e, minor first pereiopod, lateral view; f, distal portion of same, alternate lateral view. Scale bar = 1 mm for a, b, c, d; 1.2 mm for e; and , 0.24 mm for f.

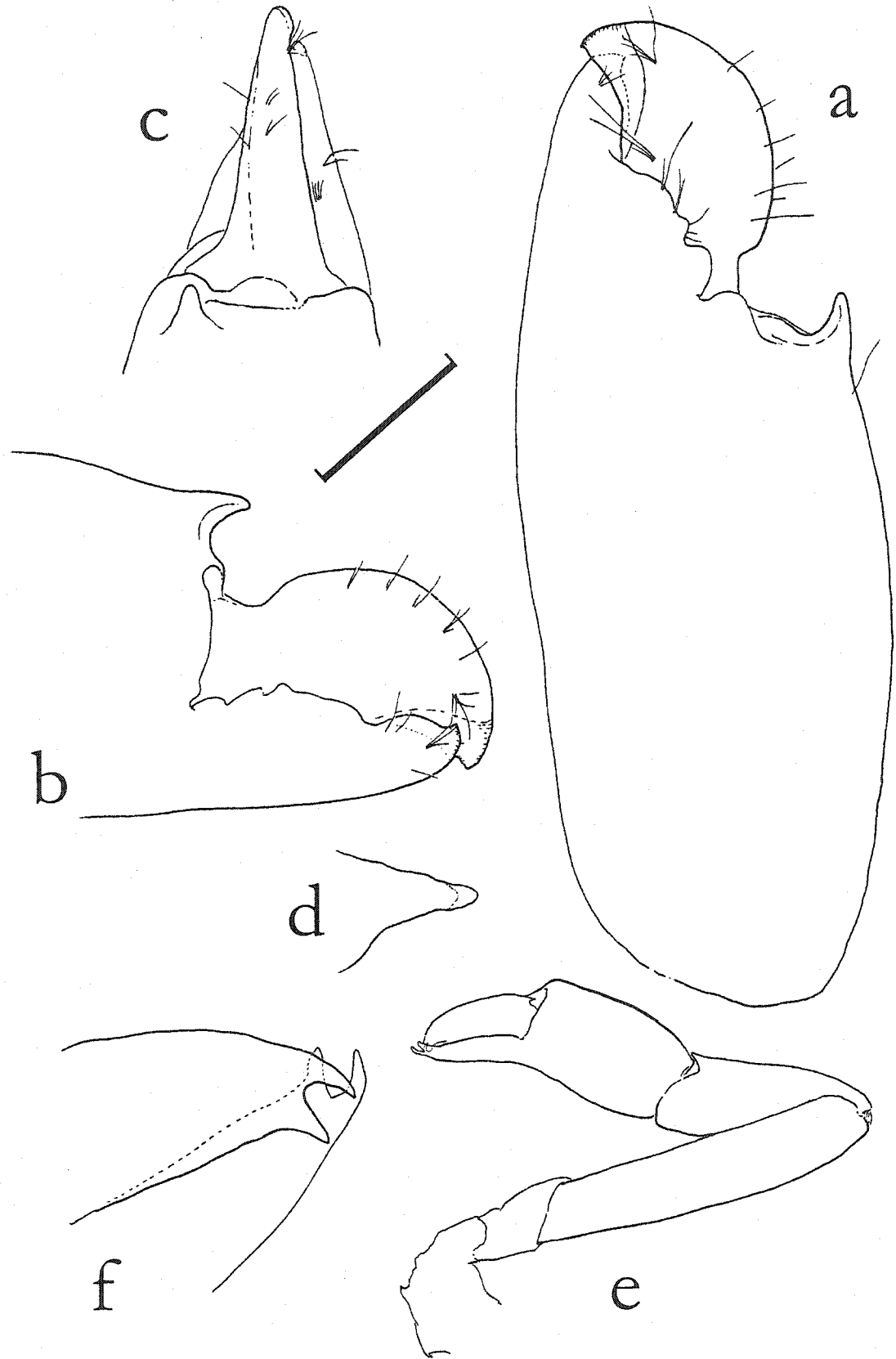


Figure 2-14. *Synalpheus* sp. 3, new species. Mouthparts. Paratype male 4.7 mm (USNM 1019049): a, mandible; b, first maxilla; c, second maxilla; d, first maxilliped; e, second maxilliped; f, third maxilliped; g, same, detail of tip. Scale bar = 0.5 mm for a, b, c, d, e; 1 mm for f; and 0.2 mm for g.

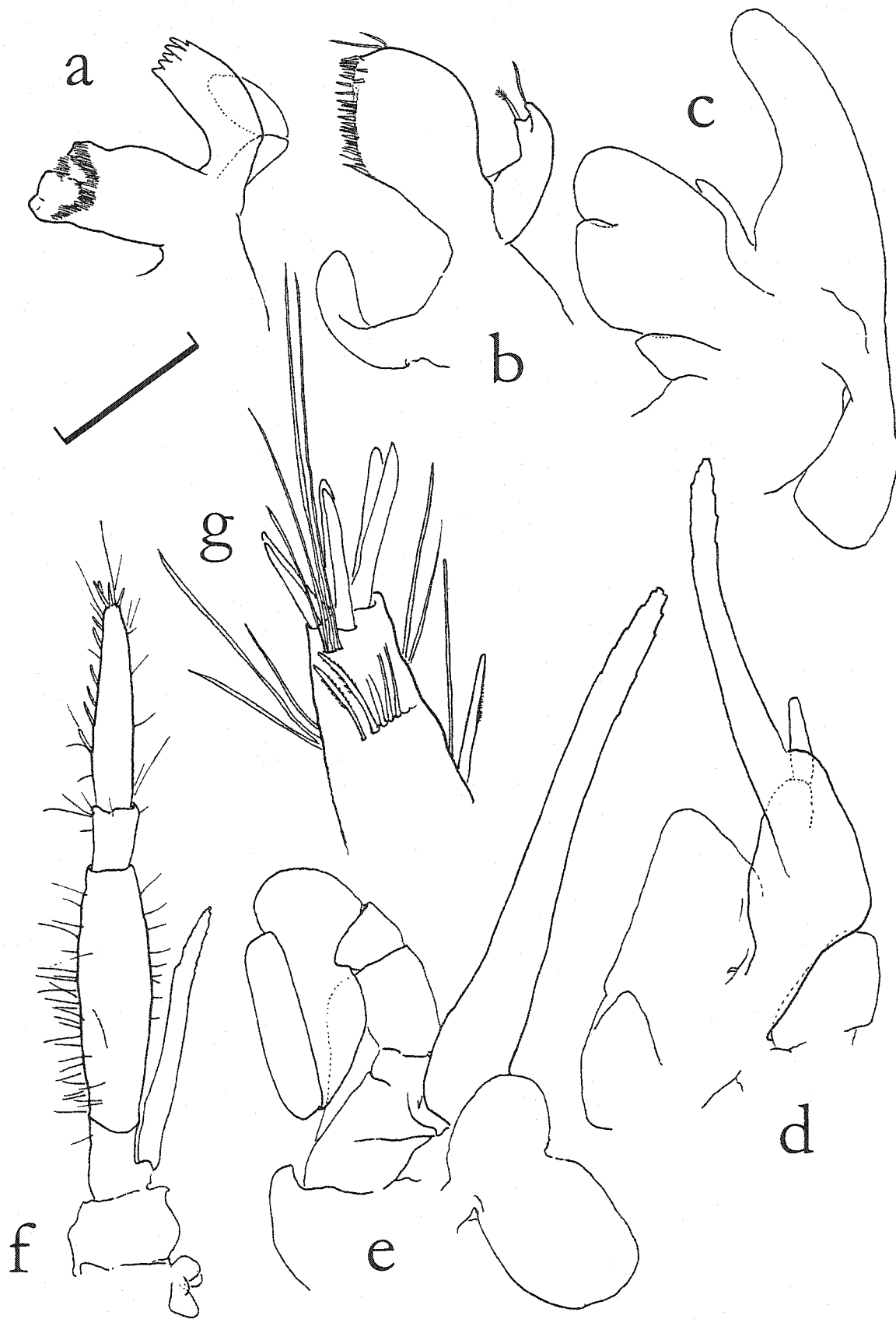


Figure 2-15. *Synalpheus* sp. 3, new species. Paratype male 4.7 mm (USNM 1019049): a, third pereiopod; b, same, detail of distal portion; c, fourth pereiopod; d, same, detail of distal portion; e, fifth pereiopod; f, detail of distal portion; g, second pereiopod. Scale bar = 1 mm for a, c, e, g; and 0.2 mm for b, d, f.

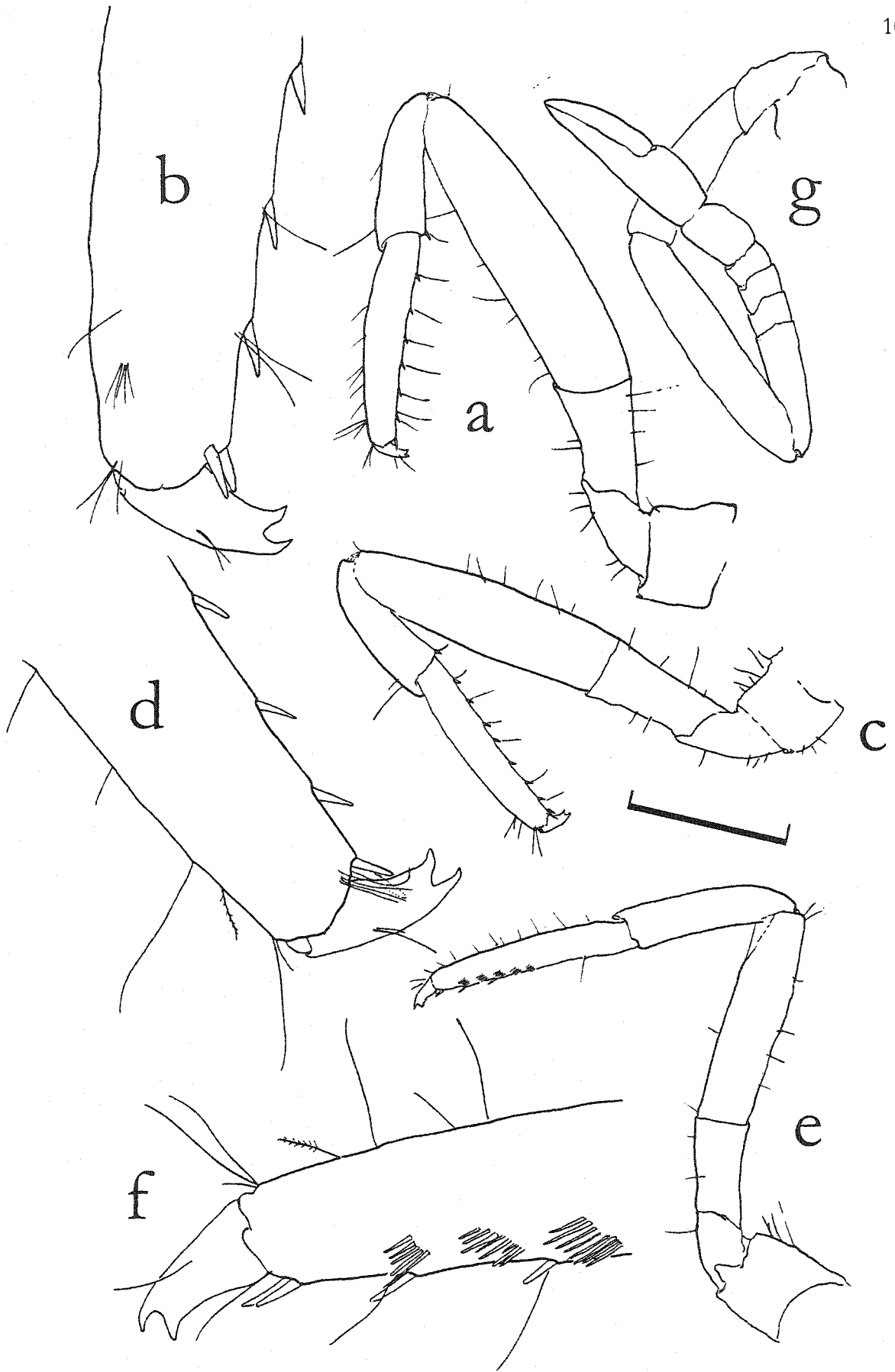
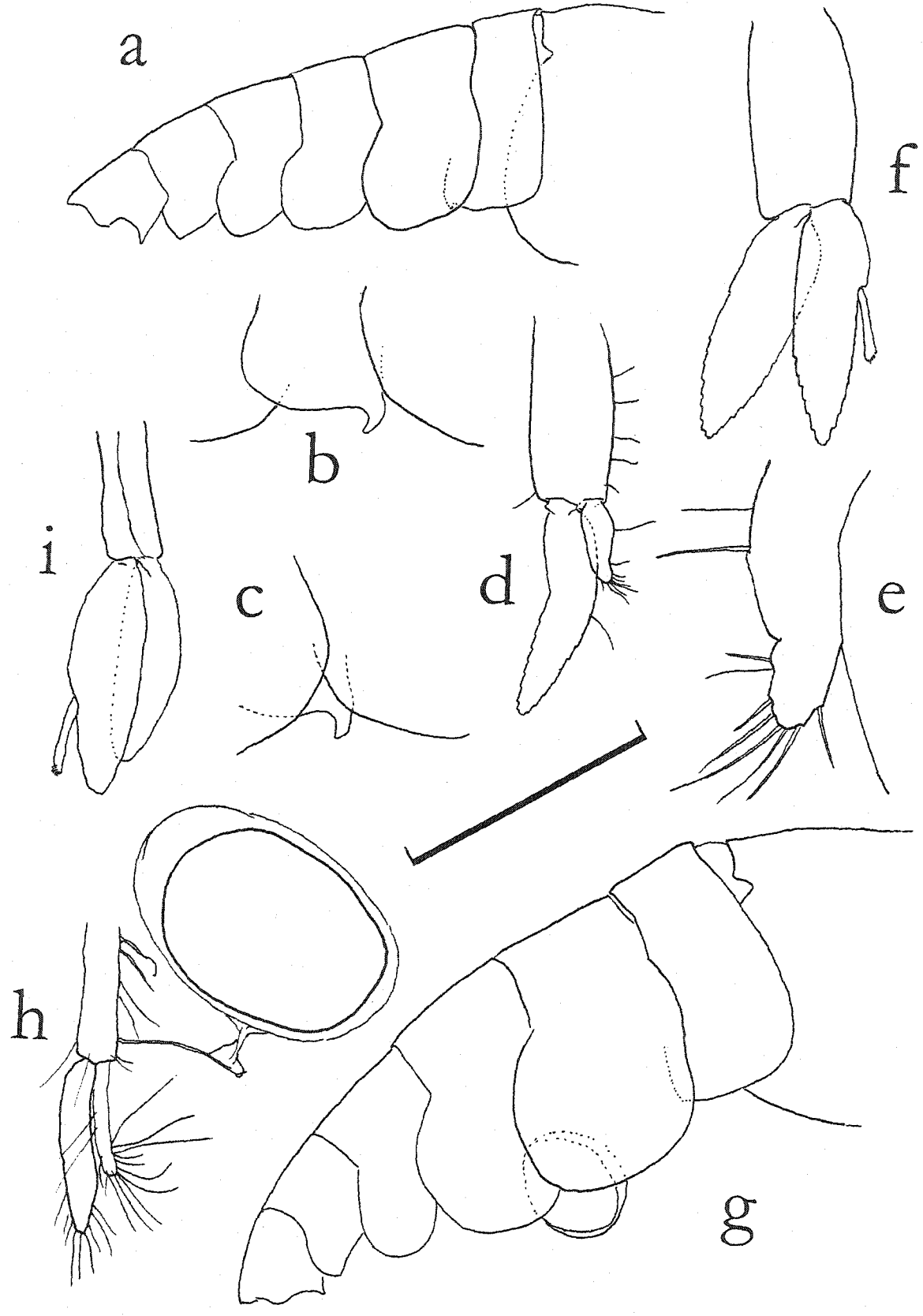


Figure 2-16. *Synalpheus* sp. 3, new species. Holotype male 5.0 mm (USNM 1019047): a, abdomen, lateral view. Paratype male 4.3 mm (USNM 1019049): b, detail of first abdominal pleura, lateral view. Paratype male 4.7 mm (VIMS 01CBC8007): c, detail of first abdominal pleura, lateral view; d, first pleopod, lateral view; e, same, detail of appendix masculina; f, second pleopod, lateral view. Allotype ovigerous female 5.1 mm (USNM 1019048): g, abdomen, lateral view; h, first pleopod, lateral view; i, second pleopod, lateral view. Scale bar = 1 mm for d, f; 1.3 mm for b, c; 1.5 mm for h, i; 3 mm for a, g; and 0.3 mm for e.





**DISTRIBUTION-** Carrie Bow Cay, Belize, and the San Blas Islands, Panama.

**REMARKS-** The ecological differences that we have been able to establish between this species and *S. brooksi* Coutière, are consistently supported by a subtle suite of morphological characters including the bluntness and orientation of the conical projection overhanging the base of the dactylus in the major chela, and the consistency of the arrangement of the ornamentation of the uropodal exopods. Also, *Synalpheus* sp. 3 grows to larger size than *S. brooksi*. Interestingly, specimens collected inside a species of *Lissodendoryx* from Florida look more like *S. brooksi* than *S. sp.3*; even when host displacement might be an explanation, further work is necessary to answer this apparent contradiction.

### *Synalpheus* sp. 4, new species

Figures 2-17 through 2-21, Plate III

**TYPE SPECIMENS-** Holotype male, 6.0 mm (USNM 1019050), allotype ovigerous female, 6.1 mm (USNM 1019051), The Pinnacles (Sand Bores), SW of Carrie Bow Cay, Belize 19 March 1993 from unidentified yellow tube sponge, 2 m deep. Paratype: female, 5.0 mm (USNM 1019052), The Pinnacles (Sand Bores), SW of Carrie Bow Cay, Belize 31 March 1993, from unidentified yellow tube sponge, 2 m deep.

**DESCRIPTION OF HOLOTYPE-** Body form subcylindrical. Carapace smooth, with sparse short simple setae. Rostrum distinctly narrower and slightly longer than orbital teeth; without reaching distal margin of first segment of antennular peduncle; distally upturned; orbitorostral process absent. Pterygostomian corner produced into bluntly acute angle. Posterior margin with distinct cardiac notch. First segment of antennular peduncle without ventromesial tooth. Antenna with 2 basal ventral processes; dorsal margin of basicerite with

acute spine, lateral spine barely reaching middle of scaphocerite; latter not reaching distal margin of carpoperite, without blade, with mesial projection at base. Third maxilliped without ventrodistal spine on antepenultimate segment; remaining mouthparts as figured.

Major first pereopod massive, dactyl slightly overreaching pollex; distal superior margin of palm produced into prominent tubercle with descending spine on tip; extensor margin of merus with flat angular projection. Minor first pereopod palm longer than fingers; dactyl with opposing surface excavate, with 3 distinct teeth, subequal in length, perpendicular to dactyl axis; 12 transverse setal combs on dorsal surface; pollex with opposing surface obliquely concave, distal tooth and subdistal accessory bump; extensor margin of merus with angular projection. Second pereopod more slender than the others, with carpus 5-segmented, longer than merus. Third pereopod dactyl biunguiculate, with flexor unguis clearly stouter than extensor; propodus with 8 mobile marginal spines evenly distributed and paired mobile spines flanking base of dactyl; carpus with single distoventral mobile spine; merus without movable spines on flexor margin; mesial lamella on coxa present. Fourth pereopod very similar to third, but slightly weaker. Fifth pereopod weaker than fourth, propodus with marginal spines irregularly arranged, and with 6 combs of setae transversely arranged on distal half.

First abdominal pleura of male weakly produced on posterior corner; second to fifth pleura obtuse; first pleopod endopod with many terminal setae; origin of marginal setae on second pleopod exopod close to base. All pleura of female broadly rounded; appendix interna present on endopod of second to fifth pleopods in both sexes. Telson stout, subtrapezoidal, middle space between distal spines greater than one-third of distal margin; marginal convex lobe present; posterior corners adjacent to spines obtuse. Uropods with 2

Figure 2-17. *Synalpheus* sp. 4, new species. Holotype male 6.0 mm (USNM 1019050): a, anterior region of carapace and cephalic appendages, dorsal view; b, same, lateral view; c, telson and uropods, dorsal view; d, dactyl of major first pereiopod, dorsal view; e, pollex of major first pereiopod, ventral view; f, distal part of merus of major first pereiopod, lateral view; g, distal part of merus of minor first pereiopod, lateral view. Allotype ovigerous female 6.1 mm (USNM 1019051): h, right scaphocerite, dorsal view. Scale bar = 1.5 mm for a, b, c, g, h; and 2 mm for d, e, f.

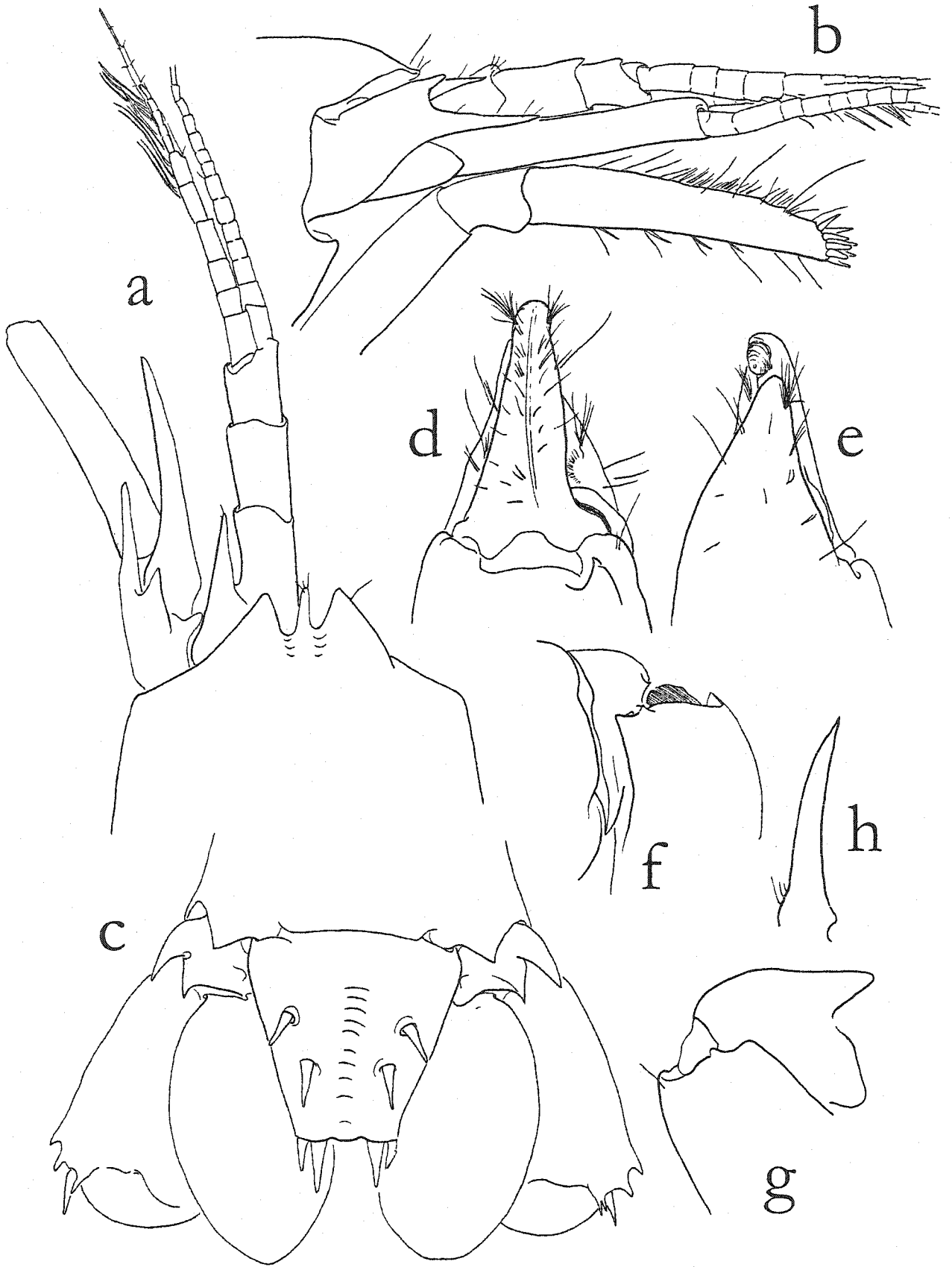


Figure 2-18. *Synalpheus* sp. 4, new species. Allotype ovigerous female 6.1 mm (USNM 1019051): a, abdomen with one egg, lateral view. Paratype female 5.0 mm (USNM 1019052): b, right first pleopod. Holotype male 6.0 mm (USNM 1019050): c, abdomen, lateral view; d, right first pleopod; e, same, detail of endopod. Scale bar = 2 mm for a, c; 1 mm for b, d; and 0.44 mm for e.

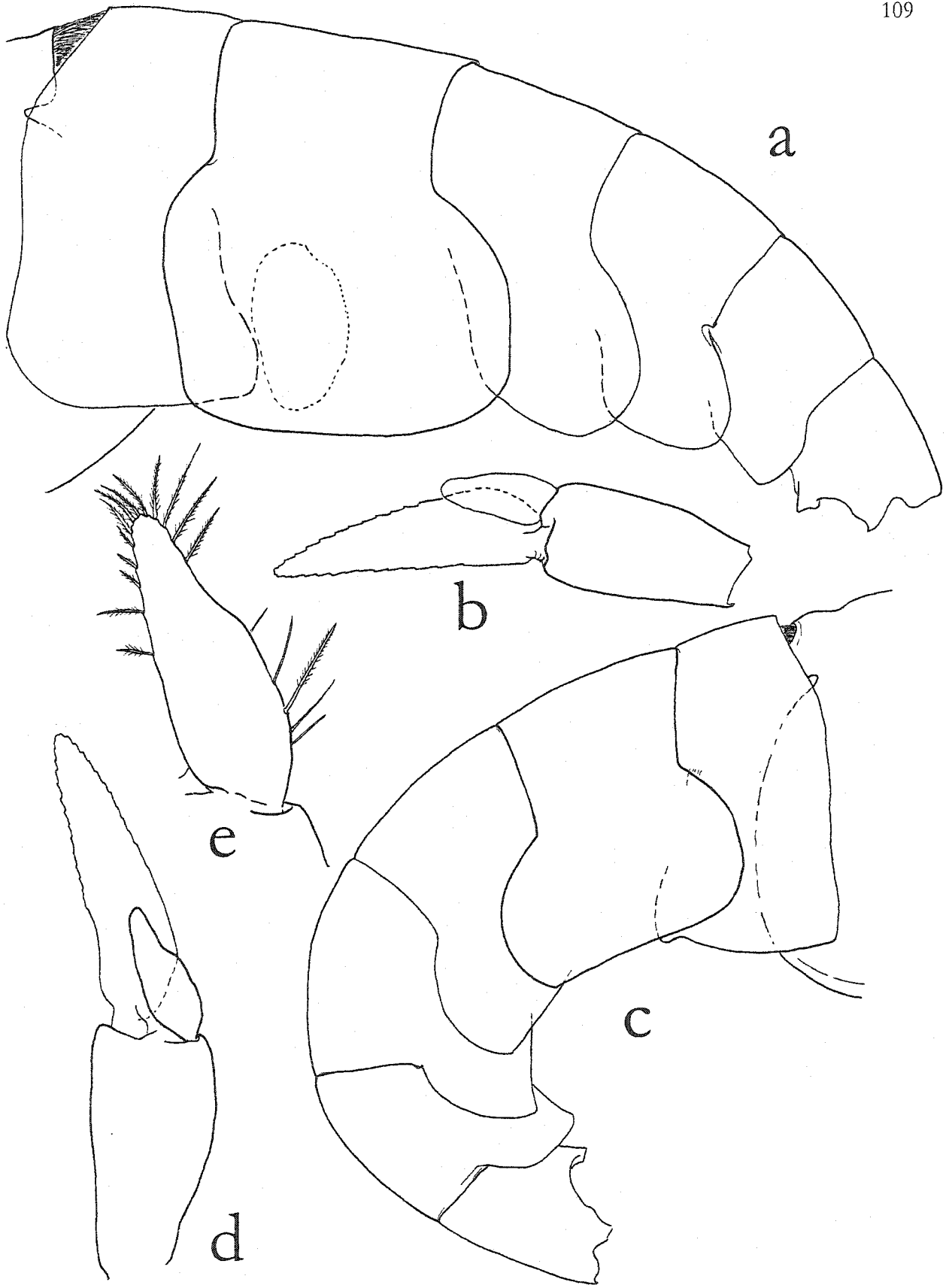
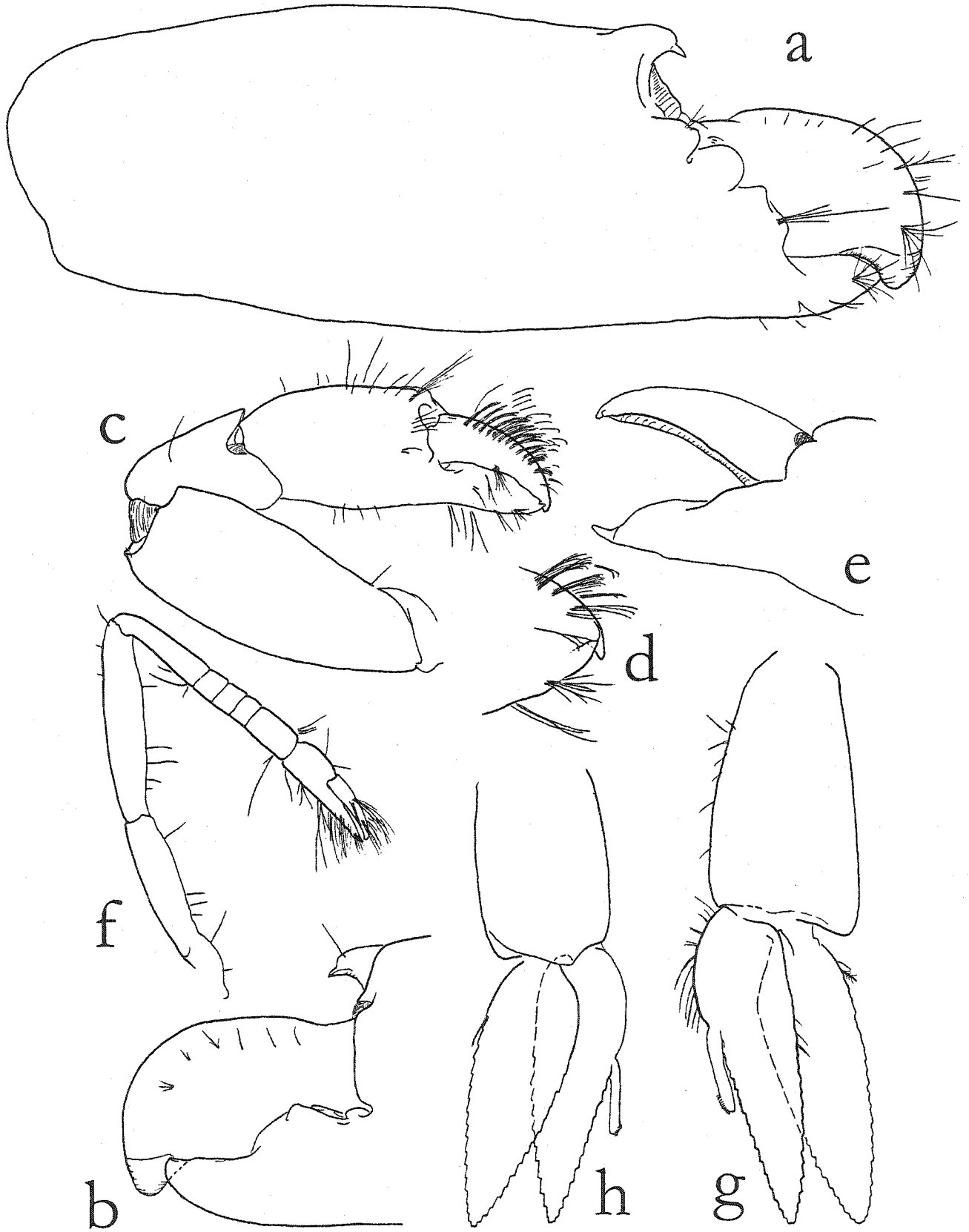


Figure 2-19. *Synalpheus* sp. 4, new species. Holotype male 6.0 mm (USNM 1019050): a, major first pereiopod in lateral view; b, same, anterior portion of external face, lateral view; c, minor first pereiopod lateral view; d, same, tip of fingers, lateral view; g, right second pleopod. Paratype female 5.0 mm (USNM 1019052): e, distal portion of minor first pereiopod, lateroventral view; f, second pereiopod, lateral view; h, right second pleopod. Scale bar = 2 mm for a, b, c, f; and 1 mm for d, 1.4 mm for d, e, g, h.





fixed teeth on outer margin of exopod; mobile spine clearly longer than adjacent mesial fixed tooth.

**COLOR-** Live specimens are translucent to dull gold with few sparse chromatophores, and distal portion of major chela brown.

**ETYMOLOGY-** It will be an honor to name this species after Dr. Brian Kensley, National Museum of Natural History, Smithsonian Institution, in appreciation of his contributions to crustacean taxonomy and his continuous support during our sampling expeditions.

**VARIATIONS-** A single slight variation, unrelated to sex or size, was recorded from the scaphocerite. Among the six specimens available (3.2-6.1 mm), three have a slight basal emargination, but only two have setae on that emargination, the remaining three show no traces of a blade or emargination. The supernumerary tooth adjacent to the mobile spine on the right uropodal exopod of the holotype is most probably a minor abnormality, not only due to its presence on a single side, but also because none of the remaining specimens possess such a character.

**ECOLOGY-** Specimens were found in the channels of an unidentified encrusting yellow tube sponge from shallow water. The sponge was almost entirely within the interior of rubble pieces.

**DISTRIBUTION-** Known only from Carrie Bow Cay, Belize.

**REMARKS-** The dissection of an embryo from the allotype suggests that the first stage is a megalopa, due to the presence of fully developed biramous pleopods and rudimentary first and second pereopods with recognizable chelae. *Synalpheus* sp. 4, new species, resembles *S. goodei*, *S. williamsi* and *S. paraneptunus*, but they can be easily separated by

Figure 2-20. *Synalpheus* sp. 4, new species. Paratype female 5.0 mm (USNM 1019052):  
a, third pereopod, lateral view; b, same, detail of distal portion; c, fourth pereopod, lateral view;  
d, same, detail of distal portion; e, fifth pereopod, lateral view; f, same, detail of distal portion.  
Scale bar = 2 mm for a, c, e, and 0.39 mm for b, d, f.

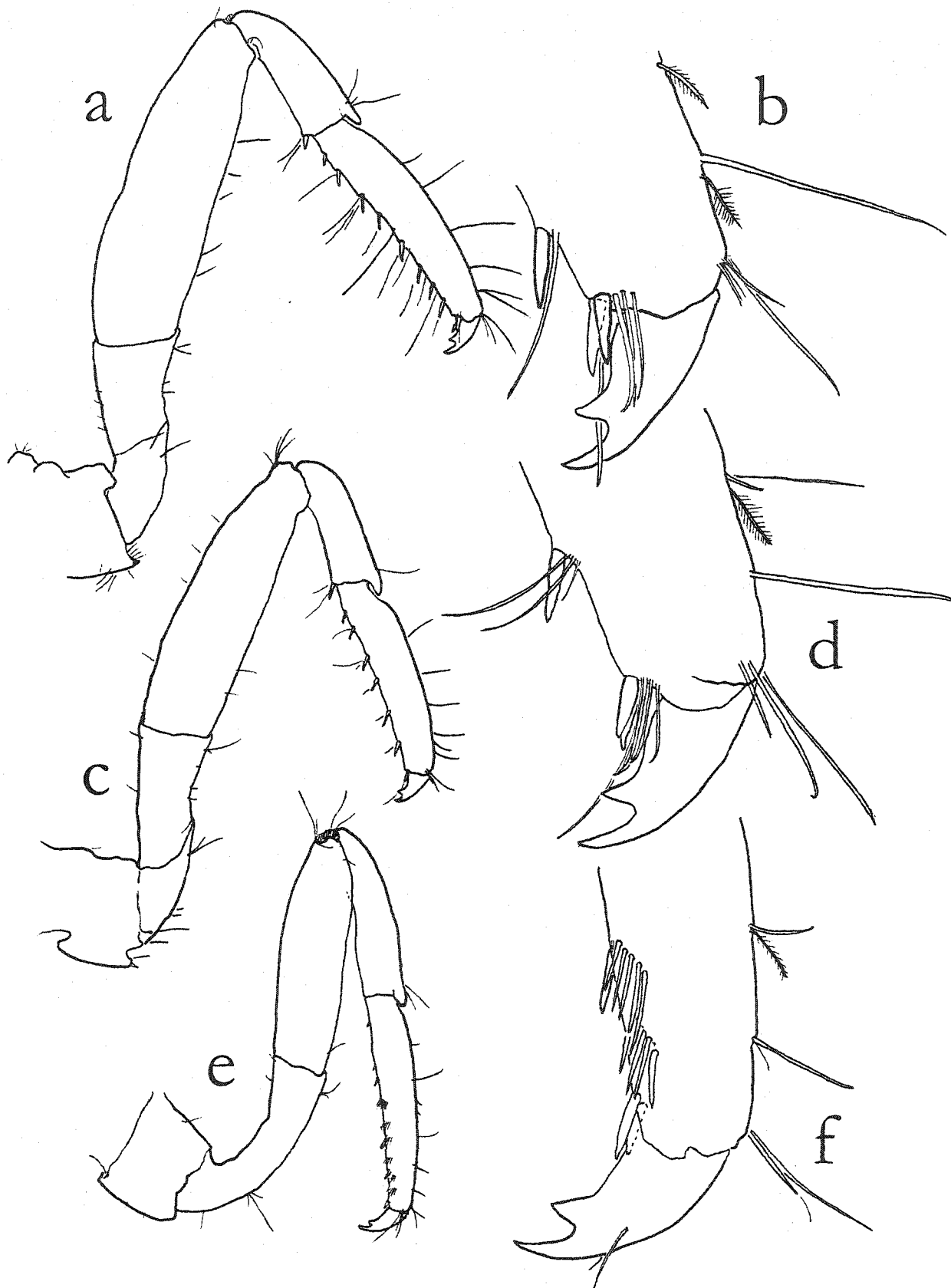
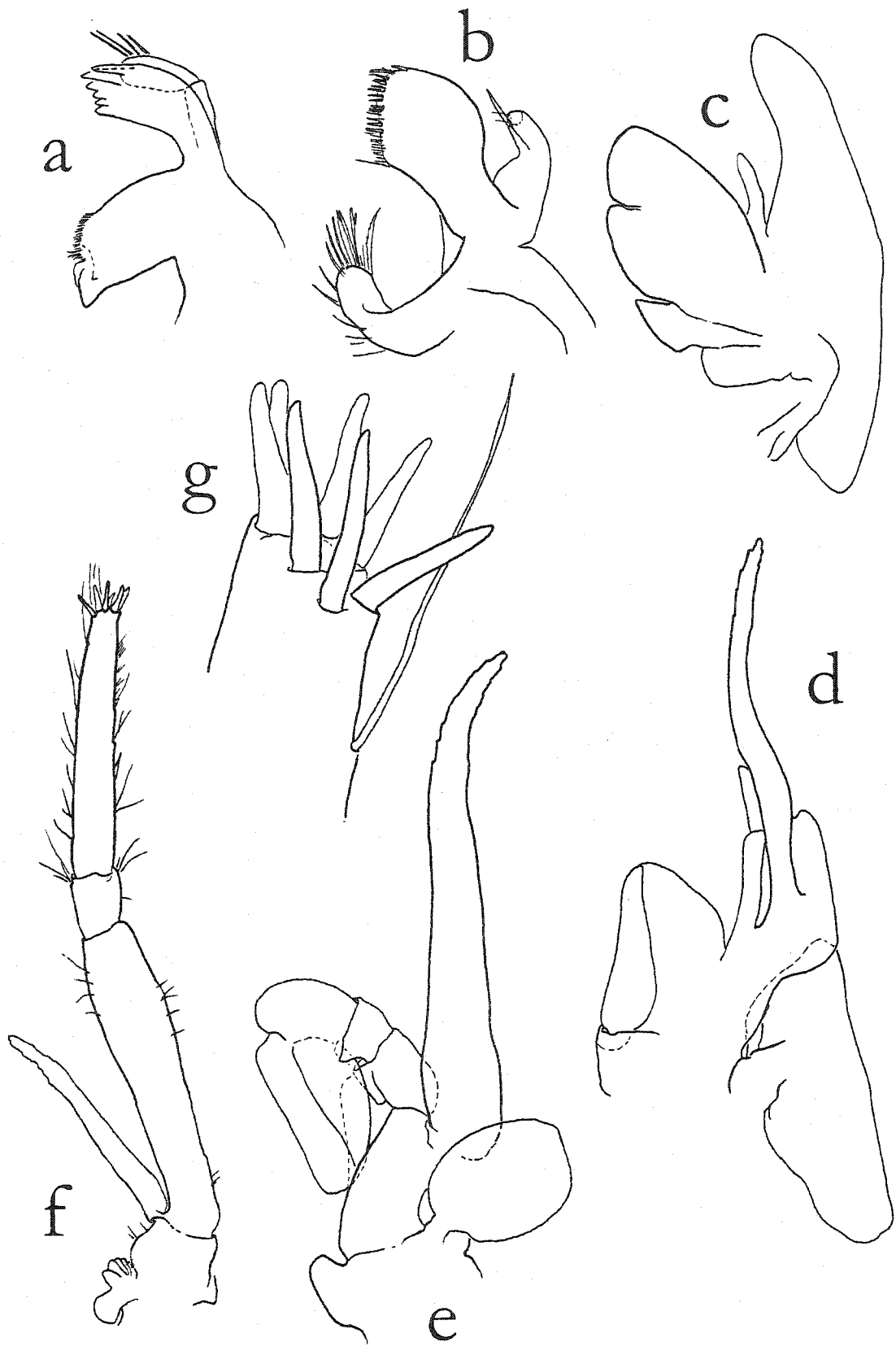


Figure 2-21. *Synalpheus* sp. 4, new species. Mouthparts. Paratype female 5.0 mm (USNM 1019052): a, left mandible; b, left first maxilla; c, left second maxilla; d, left first maxilliped; e, left second maxilliped; f, right third maxilliped; g, same, detail of tip. Scale bar = 1 mm for a, b, c, d, e, 2 mm for f, and 0.4 mm for g.



oo

f

e

d

c

b

a

several characters. In contrast to *S. sp. 4*, *S. paraneptunus* has a very reduced array of dorsal combs on the finger of the minor first chela, it has stronger apical teeth and excavate fingers in that chela, and lacks the acute spine on the upper edge of the basicerite. Both *S. goodei* and *S. williamsi* have more teeth on the outer margin of the uropodal exopod, and the first pleura of the males is strongly produced into an acute hook-like projection.

### *Synalpheus longicarpus* (Herrick, 1891)

Figure 2-22

*Alpheus saulcyi* variety *longicarpus* (Herrick, 1891) *pro pars*; Coutière 1897:369

*Synalpheus laevimanus* variety *longicarpus*: Coutière 1898a:189, 1898b:221, 1899: *passim*, 1900:357

*Synalpheus longicarpus*: Coutière, 1907:610, 1909: 53, fig. 31; Christoffersen 1979:344 *pro*

*pars*; Williams 1984:104 *pro pars*; Dardeau 1984:64 *pro pars*.

**TYPE MATERIAL-** Presumed lost, but most probably it was never properly designated (see remarks below).

**MATERIAL EXAMINED-** Male, 5.9 mm (VIMS 93CBC5506), female, 5.1 mm (VIMS 93CBC5515) Carrie Bow Cay, Belize 29 March 1993, inside *Spherospongia vesparium*, 1.5 m deep. Five males, 5.5, 6.7, 7.5, 7.5, 7.5 mm, two females, 7.9, 8.1 mm, two ovigerous females 6.7, 7.5 mm (VIMS 91NC0101), off Wilmington, North Carolina 3 July 1991, inside a yellow sponge. Five males, 5.1, 7.0, 7.3, 7.5, 7.6 mm, female, 8.4 mm (USNM 1019063), San Blas Islands, Guigalatupo reef, Panama 28 September 1993, inside *Spherospongia vesparium*, 1 m deep.

**DIAGNOSIS-** Body form subcylindrical; carapace smooth, glabrous, with pterygostomian corner produced into bluntly acute angle, and posterior margin with cardiac notch diminished.

Rostrum lanceolate, distally upturned, clearly narrower and slightly longer than orbital teeth. Orbitorostral process absent. Ocular hoods dorsally convex; in dorsal view, acute, margins straight, separated from rostrum by deep adrostral sinus. Ocular processes present, but not elongated. Ocellary beak in lateral view rod-like. Stylocerite slender; mesial margin straight, or convex; tip acute; reaching about as far as distal margin of first antennular peduncle; this latter segment without ventromesial tooth, and with 2 basal ventral processes. Basicerite without spine on dorsolateral corner, and with longer ventrolateral spine overreaching tip of stylocerite. Scaphocerite blade reduced, acute lateral spine robust, with lateral margin straight, reaching about as far as antennular peduncle; mesial projection at base of scaphocerite present. Third maxilliped with distal circlet of spines on distal segment and without ventrodistal spine on antepenultimate segment

Major first pereiopod massive, fingers shorter than half length of palm; pollex reduced, considerably shorter than dactyl; in ventral view, outer face of pollex without any protuberance. Palm of chela with distal superior margin produced into prominent tubercle with acute spine. Merus, extensor margin straight or slightly convex, with distal angular projection.

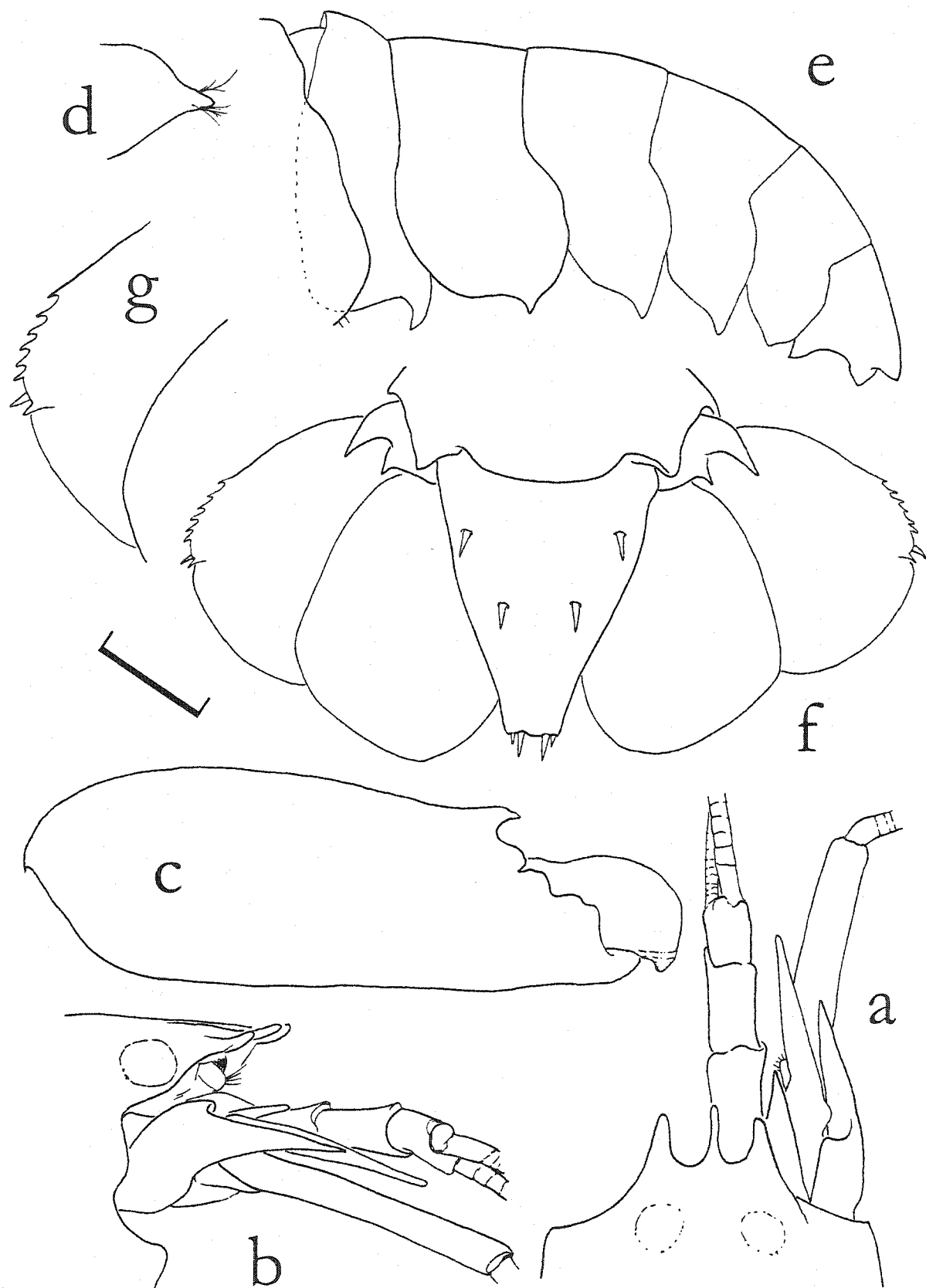
Minor first pereiopod with palm more than twice as long as high; fingers clearly shorter than palm; dactyl with opposing margin straight, blade-like, with 2 strong distal teeth, subequal in length, and parallel to dactyl axis; transverse dorsal setal combs on dactyl, very conspicuous; pollex with opposing margin straight, blade-like, with 2 strong teeth, subdistal one slightly smaller than distal one. Extensor margin of merus convex, ending in acute angle.

Second pereiopod with carpus 5-segmented, not longer than merus.

Third pereiopod slender; dactyl biunguiculate, with extensor unguis clearly thicker at base than flexor; merus without movable spines on flexor margin; mesial lamella on coxa present.



Figure 2-22. *Synalpheus longicarpus*. Male 7.6 mm (USNM 1019063): a, anterior region of carapace and cephalic appendages, dorsal view; b, same, tilted lateral view; e, abdomen, lateral view; f, telson and uropods, dorsal view; g, detail of left uropod, dorsal view. Ovigerous female 7.3 mm (USNM 1019063): c, chela of major first pereiopod, lateral view; d, same, tip of pollex, ventral view. Scale bar = 1 mm for a, b, f, 1.4 mm for c, d, e, and 0.74 mm for g.



First pleura of male with posterior corner hook-like, acutely produced ventrally and anteriorly; second through fifth pleurae of male strongly acuminate. First pleopod of male, with about six terminal setae on endopod; second pleopod of male with marginal setae on exopod originating close to base; appendix interna on second to fifth male pleopods, present. Telson, space between distal spines equal or less than one-third of distal margin; marginal convex lobe present; posterior corners adjacent to spines rectangular. Anal flaps, perianal setae, and postanal setal brush absent. Uropods with 3 to 6 fixed teeth on outer margin of exopod, slightly apart from the longer mobile spine adjacent the internal fixed tooth.

**COLOR-** Live specimens have an overall translucent straw color due to scattered chromatophores; the distal portions of the chelae have darkened (purple to black) edges; females have dull yellow ovaries; embryos are dull brick-orange.

**VARIATIONS-** One of the most frequent variations is the widening of the orbital hoods (in dorsal view), which may be associated with the larger specimens. In those instances they resemble the hoof shaped hoods in *Synalpheus* species 1. The blade on the scaphocerite is usually reduced to less than half the length of the adjacent lateral spine, but in the few occasions when it reaches beyond that point it is always ostensibly reduced. The spine overhanging the dactylar articulation on the major cheliped usually emerges at the most distal point of the protuberance, but occasionally this latter overhangs the spine, as it occurs in some other species. The number of fixed teeth on the outer corner of the uropodal exopod is most frequently from 4 to 6, but it can be anywhere from 3 up to 8. In a single specimen there was a postanal brush of stiff setae like the one in *Synalpheus* sp. 1, but less dense.

**ECOLOGY-** We have found *Synalpheus longicarpus* living only inside the canals of the loggerhead sponge *Spherospongia vesparium*, as mentioned by several authors (*e. g.* Pearse 1950,

Chace 1972, Dardeau 1984, Erdman and Blake 1987). Interestingly, according to Herrick (1891) his type specimens came from *Hircinia arcuta*, a different loggerhead sponge, currently known as *Ircinia strobilina* (Lamarck), which is superficially similar in appearance to *S. vesparium*. Given the massive dimensions that these sponges are able to attain, it is not surprising that more than one species of *Synalpheus* can be found inhabiting a single sponge; other common species in this microhabitat include *S. brooksi*, *S. pectiniger*, and occasionally *S. mcclendoni* and *Synalpheus* sp. 1.

**DISTRIBUTION-** Western Atlantic: from North Carolina throughout the Caribbean and south to Brazil. With the discovery of several new species closely related to *S. longicarpus*, the geographical boundaries of previous records under this name should be reevaluated.

**REMARKS-** This species may be recognized by the slender orbital hoods, the reduction of the cardiac notch, the relatively small spines on the dorsal surface of the telson, and by the apical insertion of the spine overhanging the dactylar articulation on the major cheliped (Table 2-1).

The largest representatives of *Synalpheus* in the western Atlantic belong to *S. longicarpus* (Herrick, 1891) and related species; consequently, it is not surprising that the name has been widely used in the literature. Yet, because the holotype designation is problematic, the history of the name is truly a quagmire. Herrick (1891:385) described the larvae of several species of Alpheidae recognizing at least two varieties in what he called *Alpheus saulcyi* Guérin; he refers to types only in his Table 1, wherein he registers his specimen number 13 as the type of his variety *longicarpus*, but he does not mention its inclusion in any Museum collection. Coutière (1898) had access to abundant material of this species, including two typical specimens sent by Herrick. The relevance of that brief contribution by Coutière (1898) resides not only in its being the first published inclusion of the species in the genus

*Synalpheus*, but the author also provided dorsal views of the anterior regions of four shrimps, two of which (his Figs. 2'' and 2''') represent the first known illustrations of *S. longicarpus*. Additional evidence of the authority of Coutière in establishing a narrower identity of this taxon, can be found in his *magnum opus* (1899) which includes the illustration of a mandible from a type (his Fig. 153), an antennule and the minor first chela of a cotype (his Figs. 116, 123, and 241), and also the tip of the telson from another specimen (his Fig. 394).

Coutière (1907) first published the binomen *Synalpheus longicarpus*, but the species was defined later in his monograph of the American species in the genus (Coutière 1909); therein a useful diagnosis is included along with figures that have been repeatedly reproduced (Hay and Shore 1918; Verrill 1922; Williams 1965 and 1984).

Probably overwhelmed by the striking intraspecific variation in the genus and in the abundant material that he examined, Christoffersen (1979) could not fully seize the definition of the species and he decided to include *S. pandionis* Coutière as a junior synonym, but this latter was resurrected by Dardeau (1984). Christoffersen (1998) later accepted Dardeau's conclusions. Interestingly, in the figures provided both by Christoffersen (1979) and Dardeau (1984) it is possible to recognize some of their specimens as a different species (see remarks under *Synalpheus* sp. 1), as is also the case of the SEM photographs of Ray (1974). The *S. longicarpus* depicted in plate 65 from Boone (1930) is clearly a misidentification since that specimen is lacking the comb of setae on the dorsal surface of the dactyl of the smaller chela, and the uropodal exopods are barren of teeth.

Additional details of the taxonomic story of this species can be found in the general introduction of the revision of *Synalpheus* (Coutière 1909) and in Verrill (1922). No mention of the whereabouts of the type material can be found in any contribution by Coutière, and

Dardeau (1984:73) could not locate the types either. An impending designation of a neotype is beyond the scope of the present contribution, mainly because of the time consuming endeavour of proving the true inexistence of the holotype.

### *Synalpheus mcclendoni* Coutière, 1910

*Synalpheus mcclendoni* Coutière, 1910: 487, fig. 3; Chace 1972:95, fig. 33, 34; Ray 1974: 148, fig. 133-135; (*nec* ?) Dardeau 1984: 74, fig. 37-39

**TYPE MATERIAL-** Three syntype males, 3.4-4.2 mm (USNM 40018) (rostrum excluded, Christoffersen 1984), Dry Tortugas, Florida, J. F. McClendon, coll. A lectotype will be designated (Ríos, in prep.).

**MATERIAL EXAMINED-** Male, 3.2 mm (USNM 1019064), Carrie Bow Cay, Belize, 5 April 1993, inside unidentified yellow boring sponge, 2.5 m deep.

**DIAGNOSIS-** Body form subcylindrical; carapace smooth, glabrous, with pterygostomian corner forming obtuse angle, and posterior margin with cardiac notch distinct.

Rostrum triangular, somewhat narrower and slightly longer than orbital teeth, not conspicuously upturned, and sometimes with a shallow ventral convex keel behind the base. Orbitorostral process absent. Ocular hoods dorsally convex; in dorsal view, acute, separated from rostrum by deep adrostral sinus. Ocular process small, but prolonged backwards into distinct keel on mesioventral edge of eye. Ocellary beak in lateral view rectangular. Stylocerite strong; mesial margin slightly concave; tip blunt; slightly overreaching distal margin of first segment of antennular peduncle; this latter segment with ventromesial tooth, and with 2 basal ventral processes. Basicerite with superior corner not prolonged and with long ventrolateral spine slightly overreaching tip of stylocerite. Scaphocerite blade present, longer acute lateral

spine robust, clearly overreaching antennular peduncle; mesial projection at base of scaphocerite present. Third maxilliped with distal circlet of spines on distal segment and without ventrodistal spine on antepenultimate segment

Major first pereiopod massive, chela elongated, fingers about half length of palm, flattened, curved inwards, and tips crossing; in ventral view, outer face of pollex without any protuberance. Palm of chela with distal superior margin typically tapering into strong acute spine. Merus, extensor margin strongly convex, with distal flat angular projection.

Minor first pereiopod with palm about twice as long as high; fingers shorter than palm; dactyl with opposing margin blade-like, subdistal accessory tooth, and 2 cants, in addition to distal tip; transverse dorsal setal combs on dactyl, very conspicuous; pollex with opposing surface blade like, and subdistal cant in addition to distal tip. Extensor margin of merus slightly convex, ending in right angle.

Second pereiopod with carpus 5-segmented, about as long as merus.

Third pereiopod slender; dactyl biunguiculate, with flexor unguis thicker than extensor; merus without spines; mesial lamella on coxa present. Pereiopods 4 and 5 normal.

First pleura of male with posterior corner obscurely produced ventrally and anteriorly into small hook-like tooth; second pleura of male broadly rounded. First pleopod of male, with about four terminal setae on endopod; second pleopod of male with marginal setae on exopod originating near midpoint; appendix interna on second to fifth male pleopods, present. Telson, space between distal spines greater than one-third of distal margin; marginal convex lobe present; posterior corners adjacent to spines obtuse. Anal flaps absent. Perianal setae absent. Postanal setal brush absent. Uropods with a single fixed tooth on outer margin of exopod, about as strong as fixed inner tooth, but shorter than slender mobile spine.

**COLOR-** In life, this shrimp has a general transparent background; major chela with prominent red chromatophores on dorsal surface of palm; thick cuticle on distal portion of palm, blue; fingers, faint brown; sparse chromatophores internally on thoracic region, cuticle faintly blue, gold where thick. A single specimen from Panamá differed strikingly from others in having an overall creamy uniform yellow to white background color with some yellowish wash on distal portions of the major chela.

**VARIATIONS-** The ocular hoods are usually straight, but occasionally in some specimens they look as Ray (1974) remarked: "they show a slight inward curving with their inner surfaces slightly sloping mesoventrally". The stylocerite usually reaches the midpoint of the second segment of the antennular peduncle, but sometimes it barely overreaches the first segment, as in Figure 3n of Coutière (1910) and Figure 33b of Chace (1972). The superior border of the palm of the major chela typically tapers into a streamlined point, but in a couple of individuals there was a basal constriction on the distal spine.

One male had two major chelae on the first pair of pereopods. To our knowledge this is the only record of this kind of abnormal symmetry in any species of *Synalpheus*. Females with two minor chelae have been observed (Duffy and Macdonald 1999) in some of the eusocial species, such as *S. filidigitus*.

**ECOLOGY-** We have found *Synalpheus mclendonii* living inside an unidentified yellowish boring sponge lining smooth cylindrical canals in coral rock; interestingly, other macroscopic encrusting sponges were virtually absent in the area.

**DISTRIBUTION-** Western Atlantic: Tobago, Panamá, Belize, Florida.

**REMARKS-** Recognizing its similarity to *Synalpheus sanctithomae*, Coutière (1910) erected *S. mclendonii* succinctly. He narrowed the description to some of the characters that would



distinguish the two species, and included only five illustrations of the new species: carpocerite, major chela (lateral view), minor chela, third leg, and anterior region (dorsal view). Chace (1972) further complemented the knowledge of this species with a full set of drawings, but, in what appears to be a mere typographical error, his key to the species introduced an unfortunate misunderstanding. In couplet 9, Chace (1972) separates *mcclendoni* from *sanctithomae*, among other characters, on the basis of the shape of the major chela; he states that it is "not noticeably twisted" in *mcclendoni* and "twisted" in the second species. However, the opposite is the true situation. Couzière (1910) explicitly mentioned that the fingers of the major chela are curved inwards in *S. mcclendoni*, and this is what gives the chela the twisted appearance noticed by Chace (1972). Ray (1974) gave an extended diagnosis of *S. mcclendoni*, mentioning the inward curvature of the fingers of the major chela; he also included SEM pictures of dorsal views of both the anterior region and the tail fan, and a lateral view of the anterior portion of the major chela. His figure 134 (Ray 1974) shows the typical elongated fingers and conical spine overhanging the articulation of the dactyl. Dardeau (1984) did not emend the aforementioned important confusion, and without any comment he changed the spelling of the specific name to "*macclendoni*". Ironically enough, it seems that the specimens he designated in that manner belong to an as yet undescribed species; he mentioned that the material he examined, syntypes included, differ from the specimens studied by Chace in several features: the palmar spine on the major chela and the first pleura of males. Both of these characters are variable in *S. mcclendoni*, but other details, such as color and host preferences, suggest that there is indeed a second species. The question of which of the species should retain the name *S. mcclendoni* awaits a closer examination of the type material deposited in the USNM. Remarkably, figure 3n in

Coutière (1910) depicts a scaphocerite shorter than the ones we observed, which were more similar to figure 33b in Chace (1972).

At Carrie Bow Cay we have collected that undescribed species; it is morphologically very similar to *S. mcclendonii*, but with a strikingly different color pattern (blue, white and red) on the major chela. Coinciding with most of the specimens examined by Dardeau (1984), these shrimp were living inside a sponge in the genus *Agelas*.

### *Synalpheus pandionis* Coutière, 1909

Figures 2-23 through 2-24, Plate IV

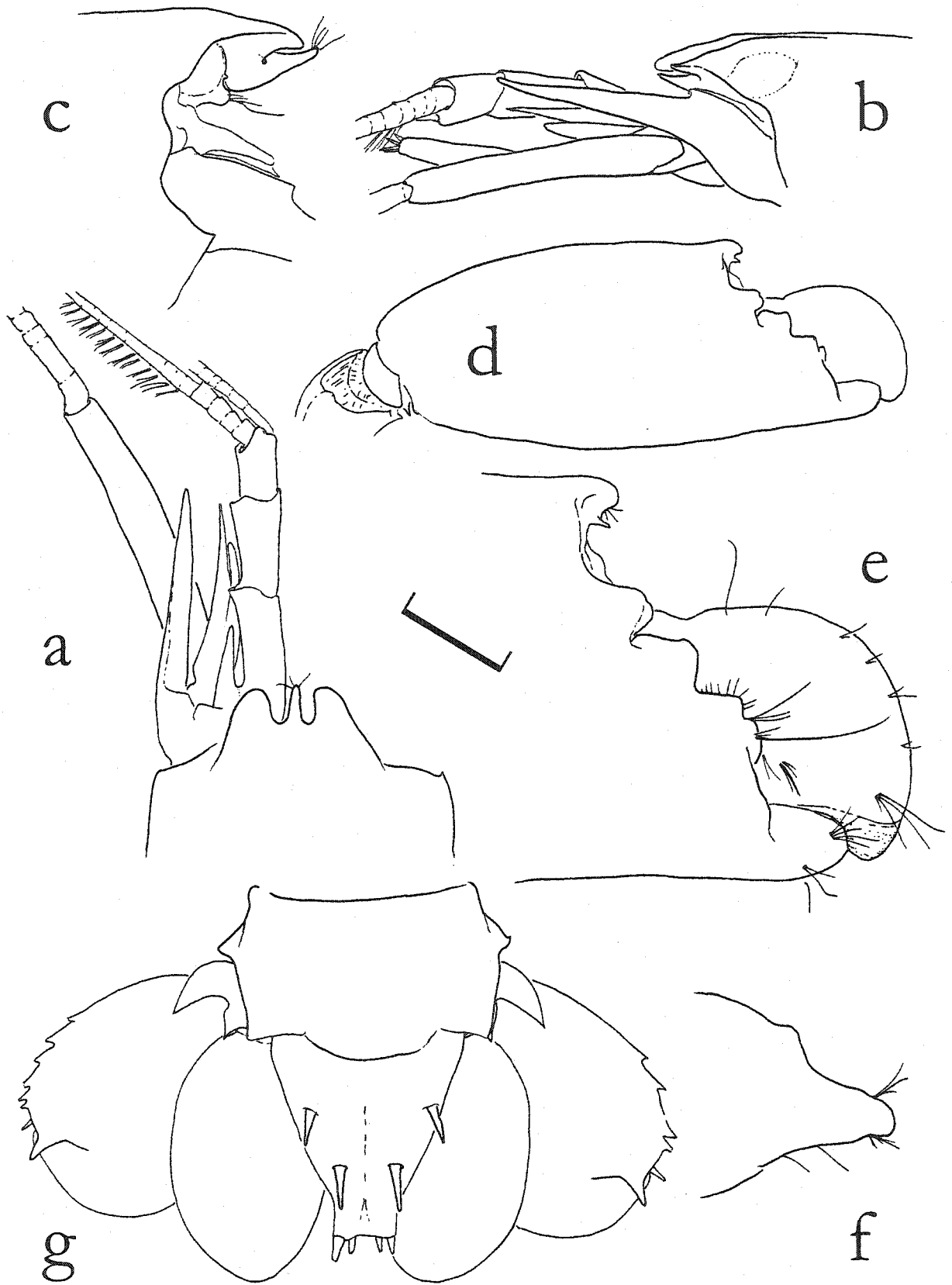
*Synalpheus pandionis* Coutière, 1909:67, fig. 39

*Synalpheus pandionis extentus* Coutière, 1909:69, fig. 40

**TYPE MATERIAL-** There are five syntypes (USNM 38400), three females and two males, Off Saint Thomas, 6 February 1899, 20-23 fms. The best preserved female has been designated as the lectotype (Ríos, in prep.).

**MATERIAL EXAMINED-** Male, 5.9 mm (USNM 1019065), ovigerous female, 6.8 mm (USNM 1019066), Carrie Bow Cay, Belize 23 August 1994, inside *Lissodendoryx strongylata* (?), 14 m deep; male, 6.6 mm (VIMS 95CBC0502); female, 6.0 mm (VIMS 95CBC0502) outer ridge of Carrie Bow Cay, Belize 21 June 1995, inside *Lissodendoryx strongylata* (?), 14 m deep; male, 5.4 mm (VIMS 95CBC2002), ovigerous female, 6.2 mm (VIMS 95CBC2001), outer ridge of Carrie Bow Cay, Belize 23 June 1995, inside *Lissodendoryx strongylata* (?); male, 4.3 mm (VIMS 98CBC0101), South Water Caye, vicinity of Carrie Bow Cay, Belize, 2 December 1998, inside sponge *Hymeniacidon amphilecta*, 12 m deep.

Figure 2-23. *Synalpheus pandionis*. Male 6.6 mm (VIMS 95CBC0502): a, anterior region of carapace and cephalic appendages, dorsal view; b, same, lateral view; c, same, alternate lateral view with cephalic appendages pushed down; d, chela of major first pereiopod, lateral view; e, same, detail of distal portion, lateral view; f, same, tip of pollex, ventral view; g, telson and uropods, dorsal view. Scale bar = 1 mm for a, b, e, f, g, 0.7 mm for c, and 2 mm for d.



**DIAGNOSIS-** Body form subcylindrical; carapace smooth, with pterygostomian corner produced into bluntly acute angle, and posterior margin with cardiac notch distinct. Rostrum in dorsal view, lanceolate, about as long as ocular hoods, but clearly narrower; in lateral view, distally upturned, with a ventrally convex longitudinal septum behind the base. Latter not reaching beyond half the height of the eye. Inferior edge of ocular hoods converging to about half the height of each side of septum. Ocular hoods dorsally convex; in dorsal view, squarely rounded anteriorly, margins convex, separated from rostrum by deep adrostral sinus. Ocular processes produced into a broad structure on the lower half of eye. Ocellary beak in lateral view, truncate. Stylocerite slender; mesial margin slightly concave; tip acute; distinctly shorter than distal margin of first segment of antennular peduncle; this latter segment without ventromesial tooth, and with 2 basal ventral processes. Basicerite without spine on dorsolateral corner, and with longer ventrolateral spine not reaching distal half of third segment of antennular peduncle. Scaphocerite blade elongated, acute lateral spine robust, with lateral margin slightly concave, reaching about as far as lateral spine of basicerite; mesial projection at base of scaphocerite present. Third maxilliped with distal circlet of spines on distal segment and without ventrodiscal spine on antepenultimate segment.

Major first pereiopod massive, fingers clearly shorter than half length of palm; pollex reduced, noticeably shorter than dactyl; in ventral view, outer face of pollex with an obtuse basal protuberance. Palm of chela with distal superior margin produced into prominent tubercle with acute downwardly directed spine on its ventral face. Merus, extensor margin strongly convex, with distal angular projection.

Minor first pereiopod with palm more than twice as long as high; fingers clearly shorter than palm; dactyl with opposing margin straight, blade-like, with terminal tooth flanked by 2 smaller

subdistal teeth, perpendicular to dactyl axis; transverse dorsal setal combs on dactyl, very conspicuous; pollex with opposing margin straight, blade-like, and subdistal accessory bump. Extensor margin of merus convex.

Second pereopod with carpus 5-segmented, about as long as merus.

Third pereopod stout; dactyl biunguiculate, with extensor unguis clearly more slender than flexor; merus without movable spines on flexor margin; mesial lamella on coxa present.

First pleura of male with posterior corner acutely produced ventrally; second pleura of male produced into acute angle. Appendix interna on second to fifth male pleopods, present. Telson, space between distal spines about one-third of distal margin, frequently without conspicuous convex lobe. Ventral face of telson without anal flaps nor perianal setae, only postanal setal brush present. Uropods with 3-6 teeth on outer margin of exopod; mobile spine distinctly removed from wide fixed tooth.

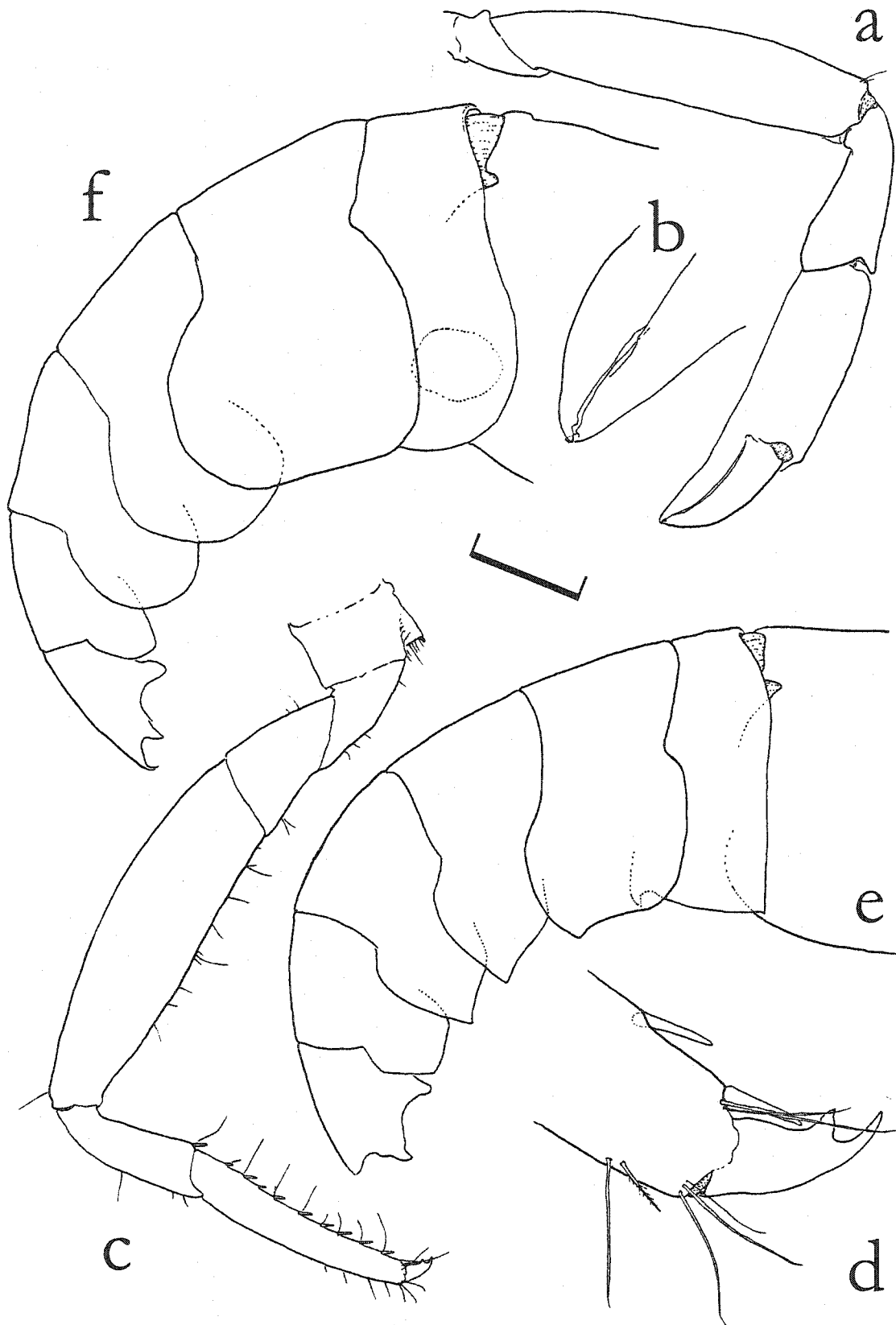
**COLOR-** Live specimens are solid uniform bright orange-red (like mature papaya), with more intense red-orange on fingers and distal portions of major chela.

**VARIATIONS-** On rare occasions, the distal margin of both the ocular hoods and the ocellary beak are not completely straight but slightly concave. The most frequent number of fixed teeth on the uropod is 4, interestingly 3 is very rare, while 5 and 6 are more common.

**ECOLOGY-** *Synalpheus pandionis* was found living in heterosexual pairs, most frequently inside a bright orange-red sponge, probably *Lissodendoryx strongylata*, other hosts include *Agelas clathrodes*, *Hyatella intestinalis* and *Hymeniacion amphilecta*. Most of the samples came from 10-15 m deep.

**DISTRIBUTION-** Western Atlantic: Florida, Belize and Caribbean coast of Panama.

Figure 2-24. *Synalpheus pandionis*. Male 6.6 mm (VIMS 95CBC0502): a, minor first pereiopod, lateral view; b, same, detail of distal portion (setal combs on dactyl omitted), alternate lateral view; c, right third pereiopod; d, same, detail of distal portion; e, abdomen, lateral view. Ovigerous female 6.8 mm (USNM 1019066): f, abdomen showing one egg, lateral view. Scale bar = 1 mm for a, c, 1.3 mm for e, f, 0.5 mm for b, and 0.2 mm for d.





**REMARKS-** The original type series of *S. pandionis* includes five specimens, all fragmented. Nevertheless, it was possible to acknowledge both their conspecificity and the series of characters that allow to distinguish this species. The most striking of these characters include: broad ocular hoods, rostrum with longitudinal posterior septum, pollex of major chela with obtuse protuberance, and the shape of the uropodal exopod. The female lectotype had the major chela still attached at the time it was designated (Ríos, in prep.). Chace (1972) made *S. grampusi* a synonym of *S. pandionis*; he chose this name despite the page location of each name in the publication by Coutière. That turned out an accurate decision, because (as Chace had remarked) the three specimens in the type series of *S. grampusi* seem to belong in two species: the two larger males, but not the smaller female, have a blade in the scaphocerite. Coutière (1909) distinguished *S. pandionis* from *S. grampusi*, based largely on the presence of that blade. Considering that both the description and the illustration of *S. grampusi* lack the blade, it is most appropriate to maintain the name *S. pandionis* for the species embellished with a blade on the scaphocerite. The female in the type series of *S. grampusi* is further considered under the remarks for *S. sp. 6*, new species.

Based on the same characters used by Coutière (1909), Christoffersen (1979) included *S. pandionis* in *S. longicarpus* (Herrick), but, as Dardeau (1984) rightfully concluded when resurrecting *S. pandionis*, these two are distinct species. Later Christoffersen (1998) recognized the validity of the two species. They can be separated by the following characters in *S. longicarpus*, including the elongated ocular hoods, the reduced cardiac notch, the lack of basal protuberance on the pollex of the major chela, the stronger distal teeth of the dactylus of the smaller chela, and the much reduced spines on the dorsal surface of the telson.

The holotype of *S. pandionis extentus* does not look much different than some of the specimens from Belize and Panama, and for this reason the subspecies is considered here as a synonym of *S. pandionis*. Furthermore, this female was apparently collected together with the type series of *S. pandionis*.

### *Synalpheus regalis* Duffy, 1996

Figure 2-25

*Synalpheus regalis* Duffy 1996b: 564, fig. 1-5.

**TYPE MATERIAL-** Male holotype (USNM 280092), 2.4 mm (rostrum excluded) from a colony of 89 males (USNM 280093 & USNM 280095) and a single ovigerous female (USNM 280094) Carrie Bow cay, Belize, 28 March 1993, inside a demosponge *Xestospongia* cf. *subtriangularis*, 15 m deep (Duffy 1996b).

**MATERIAL EXAMINED-** Thirteen males, 2.6-3.3 mm (VIMS 01CBC4803), from a colony of 258 males, and a single ovigerous female (VIMS 01CBC4806), Curlew Ridge, Belize 1 May 2001, inside sponge *Xestospongia* sp., 15 m deep.

**DIAGNOSIS-** Body form subcylindrical; carapace smooth, sparsely setose, with pterygostomian corner very obtusely angular, and posterior margin with cardiac notch distinct.

Rostrum lanceolate, about as long, but much narrower than orbital teeth, and distally upturned. Orbitorostral process absent. Ocular hoods dorsally convex; in dorsal view, squarely rounded, margins convex, separated from rostrum by deep adrostral sinus. Ocular processes virtually absent, just a slightly swollen obtuse protuberance. Ocellary beak in lateral view not rod-like. Stylocerite thick, mesial margin slightly concave, tip acute,

distinctly shorter than distal margin of first segment of antennular peduncle; this latter segment without ventromesial tooth, and with 2 basal ventral processes. Basicerite with strong sharp spine on dorsal margin, and with longer ventrolateral spine reaching about half length of second segment of antennular peduncle. Scaphocerite blade absent, acute lateral spine robust, with lateral margin slightly concave, normally not reaching distal margin of antennular peduncle; mesial corner at base of scaphocerite, obtuse. Third maxilliped with distal cirlet of spines on distal segment, and without ventrodial spine on antepenultimate segment

Major first pereiopod massive, fingers shorter than half length of palm; pollex slightly shorter than dactyl; in ventral view, outer face of pollex with obtusely subtle protuberance. Palm of chela with distal superior margin produced into prominent rounded tubercle, occasionally with accessory acute spine on distoventral face. Merus, extensor margin strongly convex, ending in obtuse angle.

Minor first pereiopod with palm less than 2 times longer than high; fingers clearly shorter than palm; dactyl simple with opposing surface obliquely concave; transverse dorsal setal combs on dactyl, very conspicuous; pollex with opposing surface obliquely concave, and no hint of second tooth. Extensor margin of merus convex, ending in obtuse angle.

Second pereiopod with carpus 4-segmented, about as long as merus.

Third pereiopod dactyl, biunguiculate, flexor unguis thicker than extensor; merus without movable spines on flexor margin; mesial lamella on coxa present. Pereiopods 4 and 5 normal.

First pleura of male with anterior corner prolonged into acute angle, and posterior corner acutely produced ventrally; second to fifth pleura of male produced into acute angle.

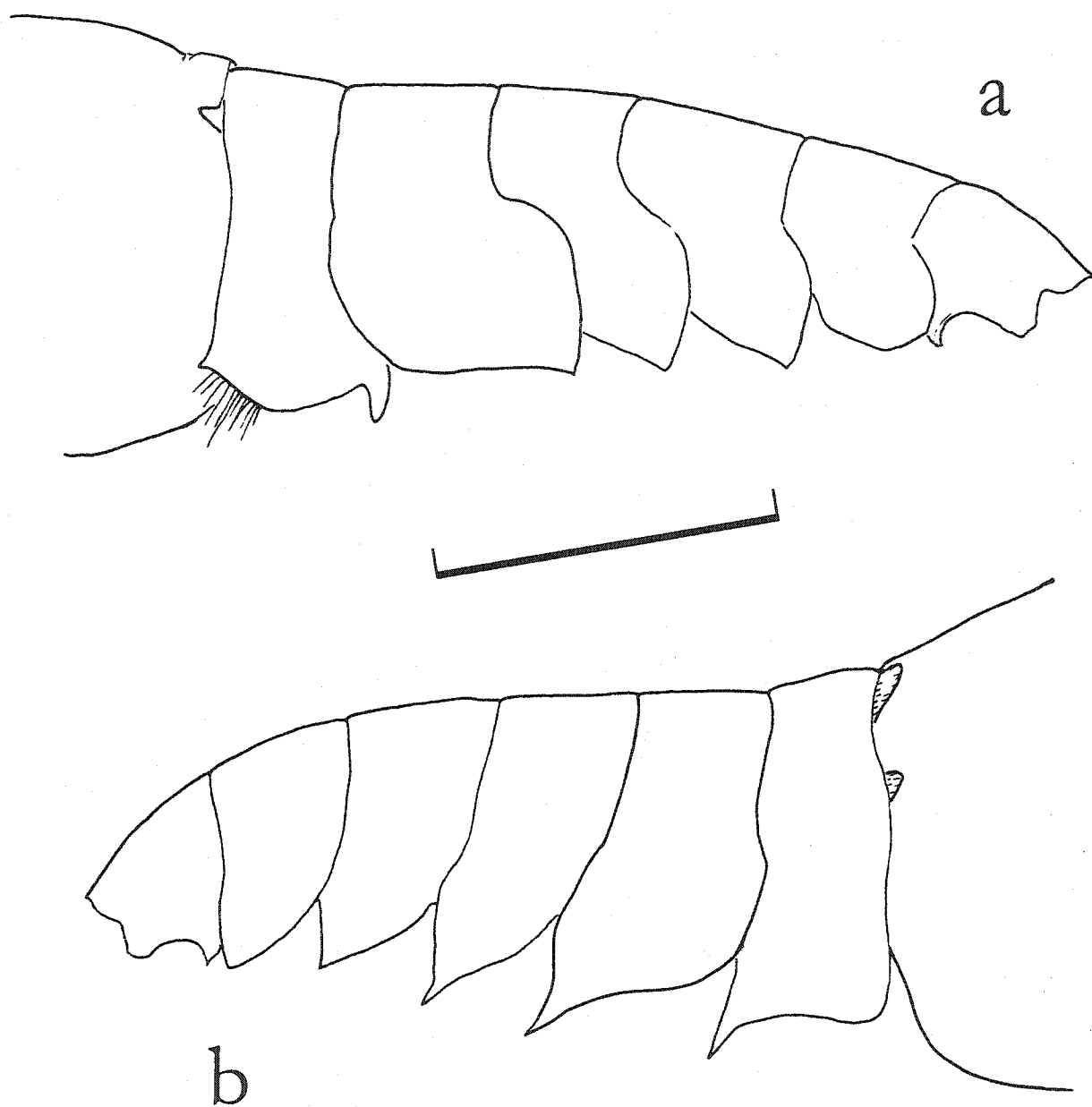


Figure 2-25. *Synalpheus regalis*. Male 2.5 mm (VIMS 93CBC4802): a, abdomen, lateral view. *Synalpheus ratbbunae*. Male 2.4 mm (VIMS 88SB12503): b, abdomen, lateral view. Scale bar = 1 mm.

First pleopod of male, with 3 or 4 setae on endopod; second pleopod of male with marginal setae on exopod originating near midpoint; appendix interna on second to fifth male pleopods, present. Telson, space between distal spines about one-third of distal margin; marginal convex lobe, absent; posterior corners adjacent to spines, obtuse. Anal flaps absent. Perianal setae absent. Postanal setal brush absent. Uropods with 2 to 4 fixed teeth on outer margin of exopod, usually removed from longer mobile spine.

**COLOR-** Live specimens are translucent orange, with sparse red chromatophores in anteriodorsal part of carapace; distal edge of palm and fingers of major chela, bright orange to brown orange; ovaries and developing embryos, pale green (Duffy 1996b).

**FIRST LARVA-** In laboratory conditions, three larvae were obtained from a wild-caught ovigerous female. The larvae were crawling megalopae very similar to those of *S. sp. 2*, but at an earlier stage. The pleopods are biramous, but unlike the ones in *S. sp. 2*, they do not have any setae. Also, the telson is less rectangular and has only the two pairs of setae on the distal margin, without any spines.

**VARIATIONS-** The anterior corner of the male first pleura normally has a ventrally oriented acute angle; only about 20% of the 212 specimens examined from a single colony had a broadly rounded corner as the one illustrated from the holotype (Duffy 1996b), and this condition usually (74%) results from a probable feminization due to abdominal parasitic isopods. The lateral spine of the scaphocerite seems to grow allometrically, it usually does not reach the distal edge of the antennular peduncle, but in the larger specimens it does reach that edge and occasionally it surpasses it slightly. The number of fixed teeth on the lateral edge of the uropodal exopod varies from 1 in the smallest specimens up to 4 or 5 in

the rare largest ones, but the most frequent numbers are 3, 2, and 4. As indicated by Duffy (1996c), some of the intraspecific variability seems to be associated with particular colonies.

**ECOLOGY-** *Synalpheus regalis* appears to live almost exclusively inside species of sponges in the genus *Xestospongia*. On a few occasions we have collected this shrimp from *Hyatella intestinalis*, *Lissodendoryx* cf. *strongylata* and *Hymeniacidon caerulea*. Eusociality in a marine animal was first witnessed in *S. regalis*. Dense populations (up to 300 individuals) of this species have a single reproductive female, distinct cohorts from a single colony are genetically related, and a certain degree of labor division has been described (Duffy 1996b, Duffy *et al.* 2002).

**DISTRIBUTION-** Western Atlantic, Belize.

**REMARKS-** There are two additional species in the western Atlantic, *S. sp. 2* and *S. rathbunae*, similar to *S. regalis*. These small shrimp are genetically distinct (Duffy 1996c) and can be separated by several morphological characters (Table 2-2). The ventral projections on the abdominal pleura in *S. regalis* are more rounded than those of *S. rathbunae* and *S. sp. 2*. The second chela has thicker fingers in *S. sp. 2* and lastly, *S. rathbunae* has an acute projection over the base of the dactyl of the major chela, instead of the more rounded protuberance of the other two species.

### *Synalpheus* sp. 5, new species

Figures 2-26 through 2-29, Plate I

**TYPE SPECIMENS-** Holotype male, 3.5 mm (USNM 1019053), allotype ovigerous female, 3.9 mm (USNM 1019054), The Pinnacles (Sand Bores), vicinity of Carrie Bow Cay, Belize, 30 April 2001, from canals of sponge *Hymeniacidon caerulea*, 2 m deep. Paratypes:

ovigerous female, 4.0 mm, two males, 3.0, 3.8 mm (VIMS 90SB1008), San Blas Islands, Panama, 13 April 1990, from rubble, 1 m deep; male, 5.1 mm, ovigerous female, 3.4 mm (VIMS 90SB0702), Porvenir and Aguadargana Islands, Panama, 12 April 1990.

**DESCRIPTION OF HOLOTYPE-** Body form subcylindrical; carapace smooth, sparsely setose, with pterygostomian corner produced into bluntly acute angle, and posterior margin with cardiac notch distinct.

Rostrum clearly narrower than orbital teeth, slightly longer than orbital teeth, and distally upturned; margins in dorsal view, straight. Orbitorostral process absent. Ocular hoods dorsally convex; in dorsal view, squarely rounded and blunt anteriorly, margins convex, separated from rostrum by deep adrostral sinus. Ocular processes present, but not elongated. Ocellary beak in lateral view not rod-like. Stylocerite slender; mesial margin slightly concave; tip acute; distinctly shorter than distal margin of first segment of antennular peduncle; this latter segment without ventromesial tooth, and with 2 basal ventral processes. Basicerite without spine on dorsolateral corner, and with longer ventrolateral spine clearly overreaching tip of stylocerite. Scaphocerite blade reduced, acute lateral spine robust, with lateral margin slightly concave, not overreaching antennular peduncle, slightly shorter than basicerite lateral spine; mesial projection at base of scaphocerite present. Third maxilliped with distal circlet of spines on distal segment and without ventrodistal spine on antepenultimate segment; other mouthparts as figured.

Major first pereopod massive, fingers shorter than half length of palm; pollex reduced, noticeably shorter than dactyl; in ventral view, outer face of pollex without pronounced protuberance. Palm of chela with distal superior margin produced into prominent tubercle

Figure 2-26. *Synalpheus* sp. 5, new species. Holotype male 3.5 mm (USNM 1019053): a, anterior region of carapace and cephalic appendages, dorsal view; b, same, lateral view; c, abdomen, lateral view; d, telson and uropods, dorsal view; e, left second pereopod. Scale bar = 1.0 mm for a, b, d, 1.5 for c, and 0.9 mm for e.



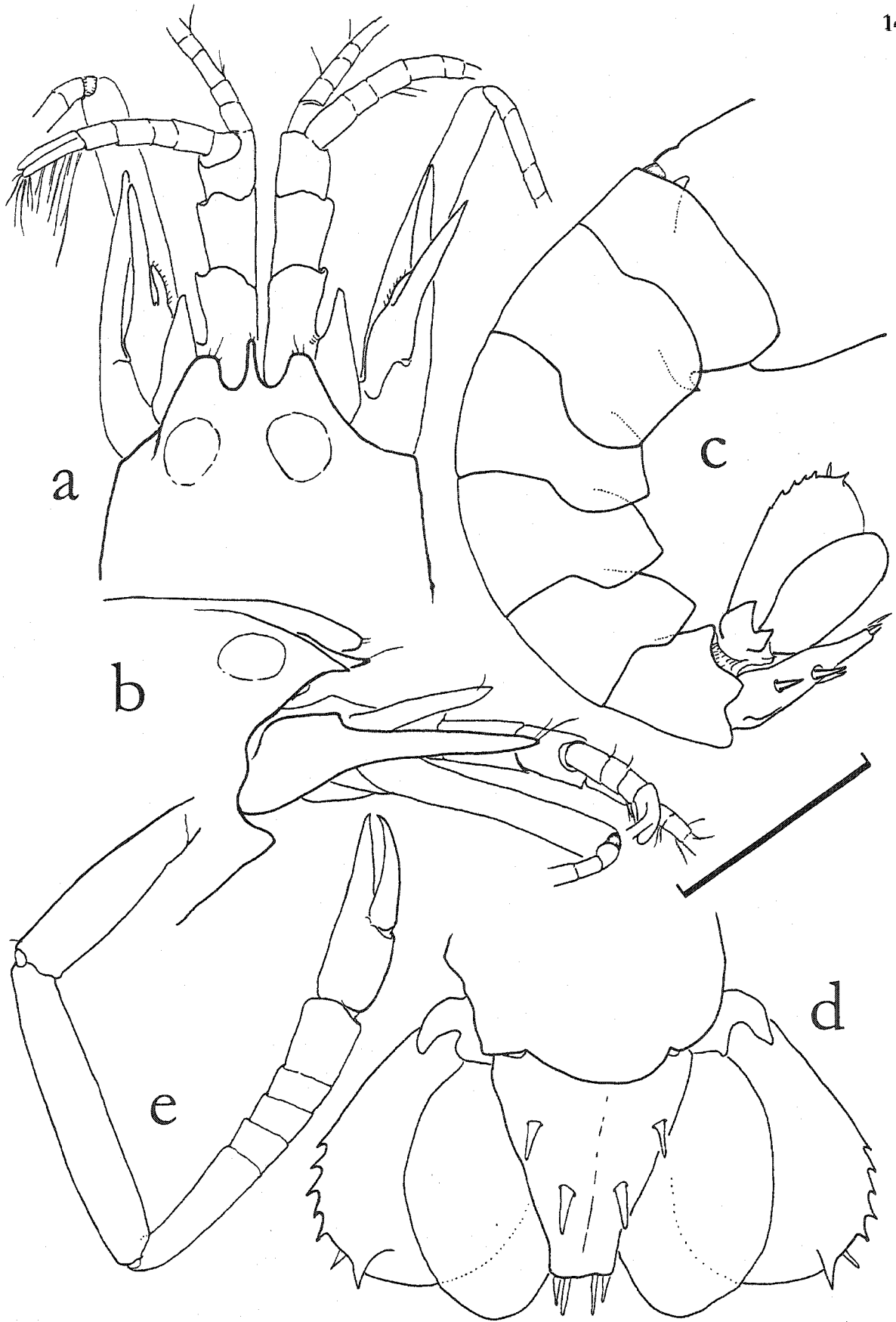
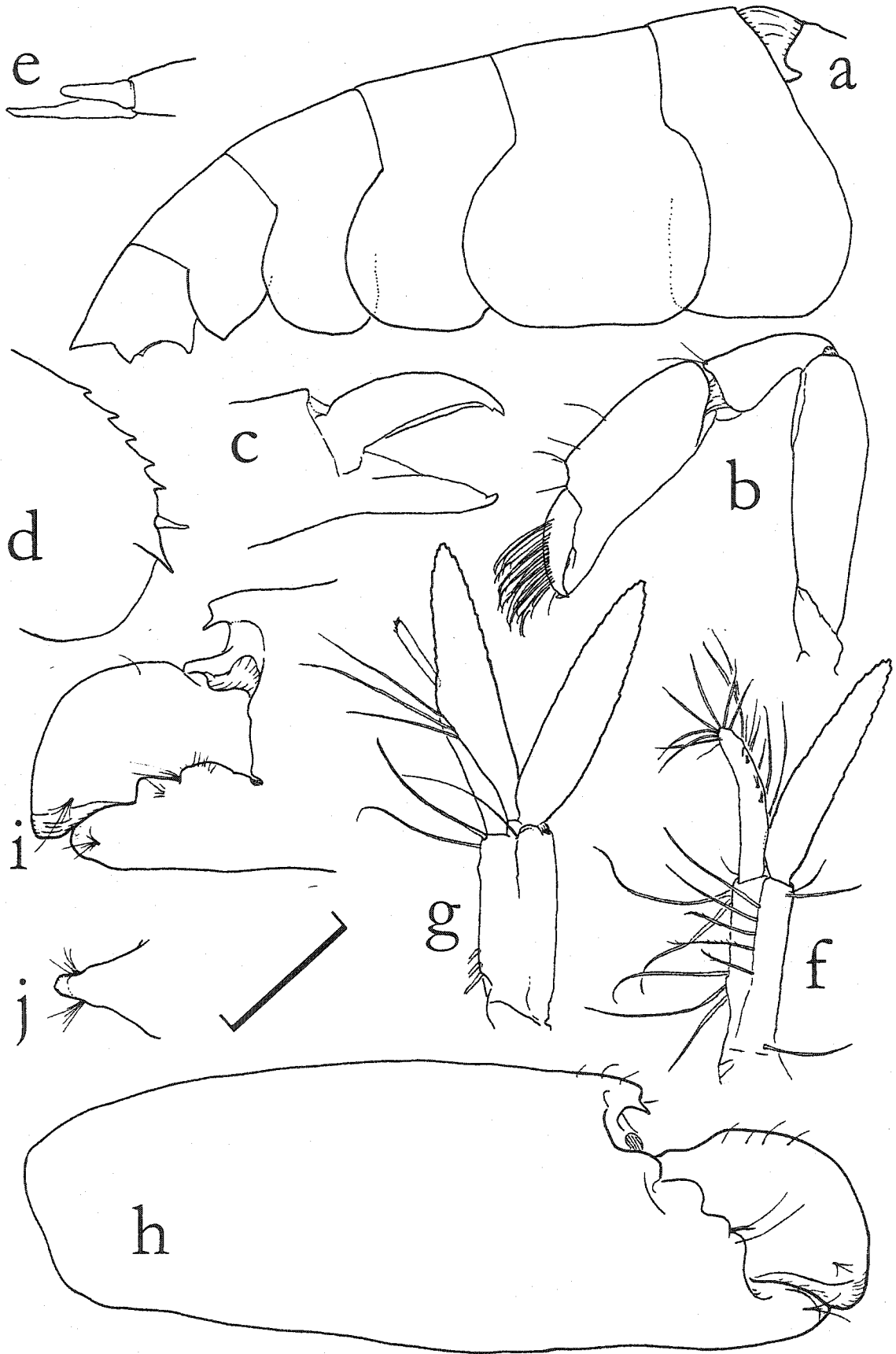


Figure 2-27. *Synalpheus* sp. 5, new species. Allotype female 3.9 mm (USNM 1019054): a, abdomen, lateral view; b, minor first pereiopod, lateral view; c, same, detail of distal portion (setal combs omitted), alternate lateral view; d, outer margin of exopod of right uropod; e, right corner of telson, lateral view; f, left first pleopod; g, left second pleopod. Holotype male 3.5 mm (USNM 1019053): h, chela of major first pereiopod, lateral view; i, same, detail of distal portion, alternate lateral view; j, same, tip of pollex, ventral view. Scale bar = 1 mm for a, b, 0.6 mm for c, f, g, 0.5 for d, e, and 0.9 for h, i, j.



with acute downwardly directed spine on its ventral face. Merus, extensor margin convex, with distal angular projection.

Minor first pereopod with palm about 2 times longer than high; fingers shorter than palm; dactyl with opposing margin straight, blade-like, with subdistal accessory protuberance parallel to dactyl axis; transverse dorsal setal combs on dactyl, very conspicuous; pollex with opposing margin straight, blade-like, and subdistal accessory bump. Extensor margin of merus convex, ending in obtuse angle.

Second pereopod with carpus 5-segmented, slightly longer than merus.

Third pereopod stout; dactyl biunguiculate, with clearly unequal ungues; and flexor unguis wider at base than extensor; propodus with nine mobile spines on flexor margin and one pair on distal end; carpus with 1 mobile distal spine; merus without any spine on flexor margin; mesial lamella on coxa present. Fourth pereopod similar to third, but weaker. Fifth pereopod similar to fourth, but slender, without distal spine on carpus, and with 7 rows of setal combs on ventral face of propodus.

First pleura of male with posterior corner distinctly produced ventrally and anteriorly, hook-like; second pleura of male with lower margin slightly concave, posterior corner broadly rounded; third to fifth pleura with posterior margin forming acute angle, not sharp. First pleopod of male, with seven terminal setae on endopod; second pleopod of male with marginal setae on exopod originating close to base; appendix interna on second to fifth male pleopods, present. Telson, space between distal spines about one-third of distal margin; marginal convex lobe present; posterior corners adjacent to spines obtuse. Anal flaps absent. Perianal setae absent. Postanal setal brush absent. Uropods with 5 fixed teeth on outer margin of exopod.

**COLOR-** Live specimens are translucent with scattered reddish chromatophores regularly distributed. The distal edges of the major chela have a dull to bright orange tone. The digestive gland is maroon-green and the eyes are white. An ovigerous female had a faint hue of white along the lateral margins of the body and bright orange ovaries.

**ETYMOLOGY-** The future specific name is a Mayan word that describes a location in a space; it could be translated as "inside" or "within, with a sense of under". It alludes to the sponge-dwelling habits of this and many other species of *Synalpheus*.

**VARIATIONS-** Several of the specimens have an abnormally reduced rostrum not reaching beyond half the length of the ocular hoods; one ovigerous female is lacking the rostrum altogether. The blade on the scaphocerite is conspicuously reduced, but always present, at least on one side, and it normally has short marginal setae throughout. In one female paratype (VIMS 90SB0702), the spine overhanging the base of the dactyl on the major chela is slightly twisted inward. The number of fixed teeth on the outer margin of the uropodal exopod varies from 4 to 6, rarely 7, with 5 teeth most frequent.

**ECOLOGY-** *Synalpheus* sp. 5 is one of several species found in canals of the midnight blue sponge *Hymeniacidon caerulea*. It has also been found inside a white unidentified soft sponge.

**DISTRIBUTION-** Belize and Caribbean Panama.

**REMARKS-** This species is closely related to *S. pandionis*, *Synalpheus* sp. 1 and *S.* sp. 6, but can be distinguished from them by the presence of a minute blade on the scaphocerite, a rounded posterior corner on the second male pleura, and ostensibly unequal spines on the posterior margin of the telson (Table 2-1). Also, full grown individuals of *S.* sp. 5 are never as large as those of the other species.

Figure 2-28. *Synalpheus* sp. 5, new species. Holotype male 3.5 mm (USNM 1019053): a, left third pereopod; b, same, detail of distal portion; c, left fourth pereopod; d, same, detail of distal portion; e, left fifth pereopod; f, same, detail of distal portion; g, left first pleopod; h, left second pleopod. Scale bar = 1 mm for a, c, e, g, h, and 0.28 mm for b, d, f.

Figure 2-29. *Synalpheus* sp. 5, new species. Mouthparts. Holotype male 3.5 mm (USNM 1019053): a, left mandible; b, left first maxilla; c, left second maxilla; d, left first maxilliped; e, left second maxilliped; f, left third maxilliped. Scale bar = 1 mm for a, b, and 1.8 mm for c, d, e, f.

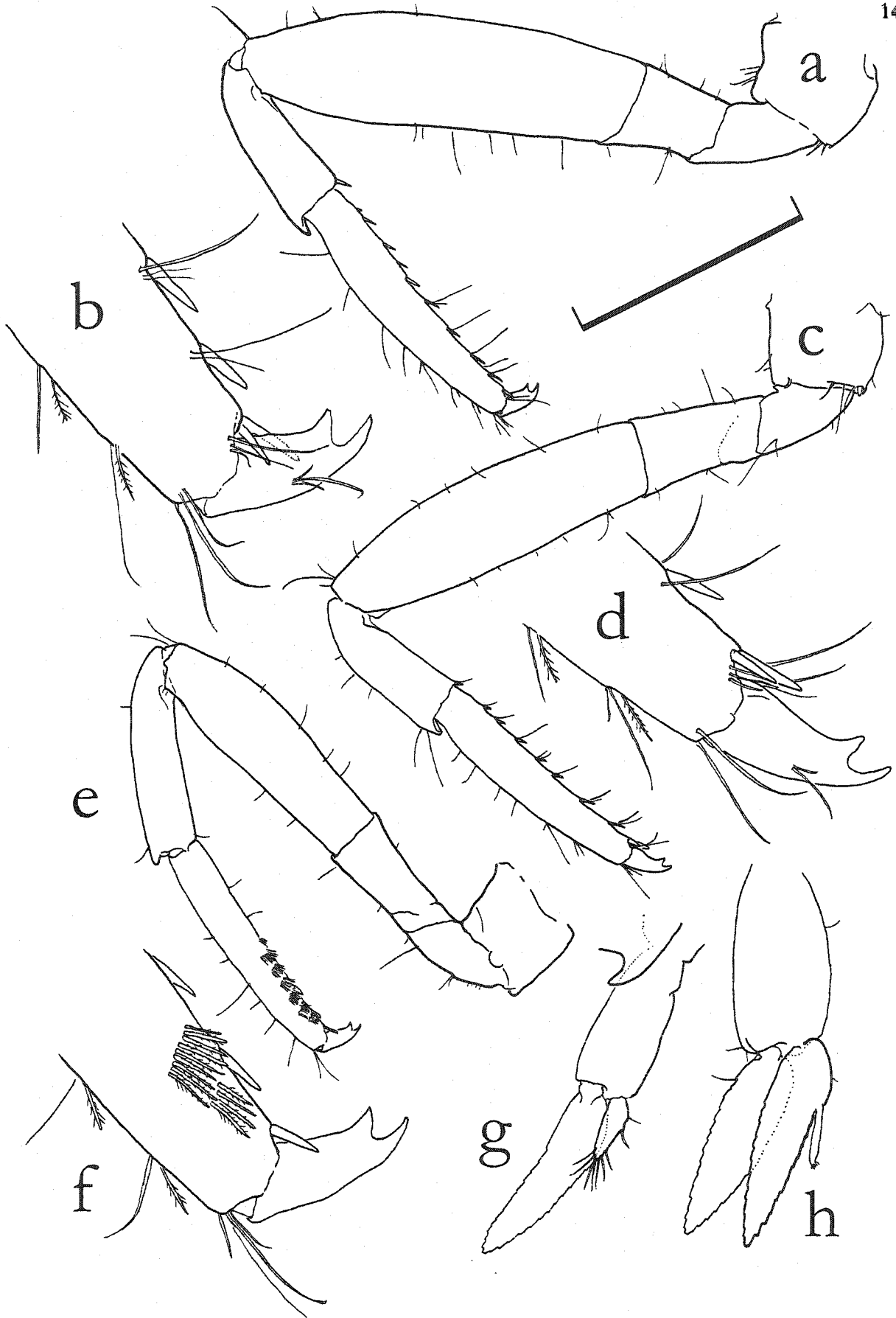


Figure 2-29. *Synalpheus* sp. 5, new species. Mouthparts. Holotype male 3.5 mm (USNM 1019053): a, left mandible; b, left first maxilla; c, left second maxilla; d, left first maxilliped; e, left second maxilliped; f, left third maxilliped. Scale bar = 1 mm for a, b, and 1.8 mm for c, d, e, f.





Some of the specimens identified as *S. grampusi* by Coutière (1909) resemble *S. sp.5*, but the predicament of trying to retain that old name would prompt more instability in the taxonomy of the genus. See additional remarks under both *S. pandionis* and *S. sp. 6*.

### *Synalpheus williamsi* Ríos and Duffy, 1999

*Synalpheus williamsi* Ríos and Duffy 1999: 541, fig. 1-6

**TYPE SPECIMENS-** Holotype male, 3.6 mm (USNM-276158), allotype ovigerous female, 4.5 mm (USNM-276159), Carrie Bow Cay, Belize, 13 June 1996, from canals of same specimen of midnight-blue sponge *Hymeniacidon caerulea*, 18 m deep. Paratypes: male, 4.4 mm, 2 ovigerous females, 4.3, 4.8 mm (USNM-276160), Carrie Bow Cay, Belize, 4 April 1993, from canals of same specimen of midnight-blue sponge *H. caerulea*, 13 m deep; Paratype male, 2.3 mm (CNCR 17987) Carrie Bow Cay, Belize, 12 June 1996, from canals of midnight-blue sponge *H. caerulea*, 18 m deep; Paratype male, 3.7 mm (MNHN-Na 13561) Ulagsukun Reef, Panamá, 17 January 1991, from canals of midnight-blue sponge *H. caerulea*.

**MATERIAL EXAMINED-** Holotype male, 3.6 mm (USNM-276158), allotype ovigerous female 4.5 mm (USNM-276159), Carrie Bow Cay, Belize, 13 Jun 1996, from canals of same specimen of midnight-blue sponge *Hymeniacidon caerulea*, 18 m. Panamá: Mamitupo Reef, San Blas Islands: 19 Jan 1991, male, 4.1 mm (VIMS), in orange tubular sponge.

**DIAGNOSIS-** Body form subcylindrical; carapace smooth, sparsely setose, with pterygostomian corner produced into bluntly acute angle, and posterior margin with cardiac notch distinct.

Rostrum about as long as, but clearly narrower than orbital teeth, and distally upturned; margins in dorsal view, straight; ventral margin convex. Orbitorostral process absent.

Ocular hoods dorsally convex; in dorsal view, acute, separated from rostrum by deep adrostral sinus. Ocular processes broad. Ocellary beak in lateral view, with inner margin concave and exterior convex. Stylocerite slender; mesial margin slightly concave; tip acute; reaching about as far as distal margin of first antennular peduncle; this latter segment without ventromesial tooth, and with 2 basal ventral processes. Basicerite with broad spine on dorsal margin, and with longer ventrolateral spine reaching distal half of second segment of antennular peduncle. Scaphocerite blade broad, slightly reduced, acute lateral spine robust, with lateral margin slightly concave, clearly overreaching antennular peduncle; mesial projection at base of scaphocerite present.

Third maxilliped with distal circlet of spines on distal segment and without ventrodistal spine on antepenultimate segment

Major first pereiopod massive, fingers clearly not longer than half length of palm; pollex reduced, much shorter than dactyl; in ventral view, outer face of pollex with a strong obtuse basal protuberance. Palm of chela with distal superior margin produced into prominent tubercle with acute spine. Merus, extensor margin strongly convex, with distal flat angular projection.

Minor first pereiopod with palm clearly less than 2 times longer than high; fingers clearly shorter than palm; dactyl with opposing surface excavate, with subdistal accessory bump perpendicular to dactyl axis; transverse dorsal setal combs on dactyl, very conspicuous; pollex with opposing surface obliquely concave, and subdistal accessory bump. Extensor margin of merus convex, with flat distal angular projection.

Second pereiopod with carpus 5-segmented, slightly longer than merus.

Third pereopod slender; dactyl biunguiculate, with flexor unguis slightly thicker than extensor; merus without movable spines on flexor margin; mesial lamella on coxa present. Pereiopods 4 and 5 normal.

First pleura of male with posterior corner distinctly produced ventrally and anteriorly into wide hook-like flap; second pleura of male broadly rounded. First pleopod of male, with 4 or 5 terminal setae on endopod; second pleopod of male with marginal setae on exopod originating close to base; appendix interna on second to fifth male pleopods, present. Telson, space between distal spines greater than one-third of distal margin; marginal convex lobe present; posterior corners adjacent to spines rectangular. Anal flaps absent. Perianal setae present. Postanal setal brush absent. Uropods with 3 to 6 fixed teeth on outer margin of exopod.

**COLOR-** Live specimens were translucent faint gold to golden brown, with tip of chelae (fingers and distal part of palm included) of first pereopods bright orange to red; second legs golden; third to fifth, transparent; and traces of blue in the gut and in the branchiae. These traces were the same dark blue as the host sponge, and they still can be seen in some of the preserved specimens (Ríos and Duffy 1999).

**VARIATIONS-** The number of immovable teeth on the lateral margin of the uropodal exopod varies from three to six, with a mode of four; this variation apparently relates to size and perhaps sex, considering that the smaller specimens have fewer teeth, and that the only 2 specimens with 6 teeth were males (Ríos and Duffy 1999).

**ECOLOGY-** *Synalpheus williamsi* lives inside the internal canals of the midnight-blue sponge *Hymeniacidon caerulea*. We have recorded occasional occurrences in a different

unidentified orange encrusting sponge of tubular shape (Ríos and Duffy 1999), and in another unidentified yellow sponge.

**DISTRIBUTION-** Western Atlantic: Belize, Panama.

**REMARKS-** Besides inhabiting different sponges, *S. williamsi* can be unequivocally distinguished from the morphologically close *S. goodii*, by several features of the latter, which include: lack of protuberance on the pollex of the major chela; a wider submesial fixed tooth, a shorter mobile spine, and more fixed teeth on the outer margin on the uropodal exopod; the presence of a tuft of setae behind the anal opening; and the absence of marginal setae around the anal opening.

### *Synalpheus* sp. 6, new species

Figures 2-30 through 2-33

**TYPE SPECIMENS-** Holotype male, 6.0 mm (USNM 1019055), allotype ovigerous female, 7.2 mm (USNM 1019056), Twin Cays, Belize, 26 April 2001 from canals of sponge *Lissodendoryx colombiensis*, 1.2 m deep. Paratypes: male, 5.3 mm (USNM 1019057), ovigerous female, 6.4 mm (VIMS 94CBC1407), Twin Cays, Belize, 20 August 1994, from canals of sponge *Lissodendoryx colombiensis*, 1.2 m deep; ovigerous female, 5.5 mm (USNM 1019058), Twin Cays, Belize, 22 August 1994, from canals of sponge *Lissodendoryx colombiensis*, 1.2 m deep; male, 5.0 mm (VIMS 98CBC0902), ovigerous female, 5.4 mm (VIMS 98CBC0901), The Pinnacles (Sand Bores), Belize, 3 December 1998, from canals of sponge *Lissodendoryx* cf. *strongylata*, 1.5 m deep.

Figure 2-30. *Synalpheus* sp. 6, new species. Paratype male 5.3 mm (USNM 1019057): a, anterior region of carapace and cephalic appendages, dorsal view; b, same, lateral view; c, abdomen, lateral view; d, minor first pereopod, lateral view; e, chela of same, alternate lateral view. Paratype ovigerous female 5.5 mm (USNM 1019058): f, abdomen showing two eggs, lateral view. Scale bar = 1.4 mm for a, b, and 1 mm for c, d, e, f.

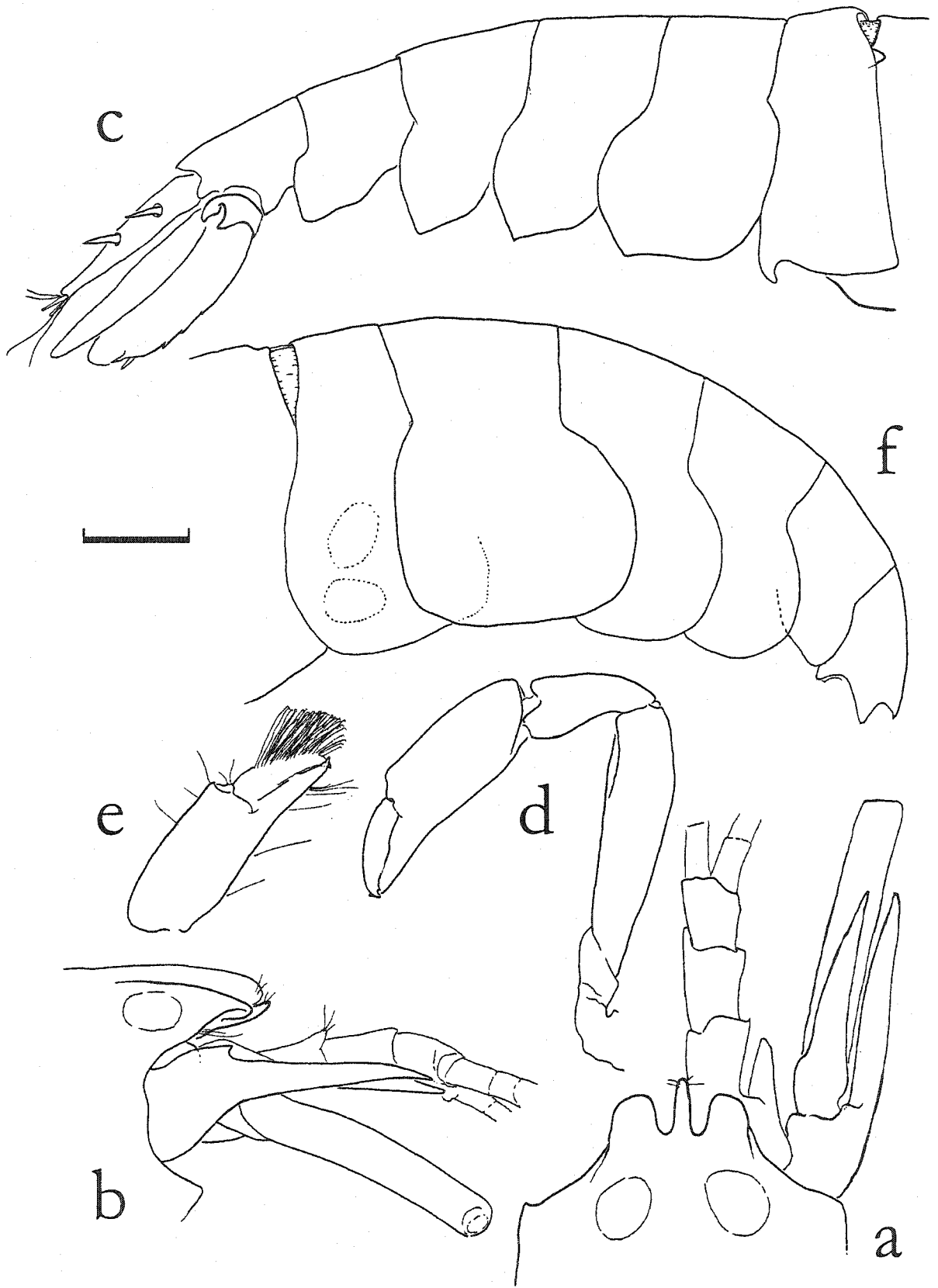
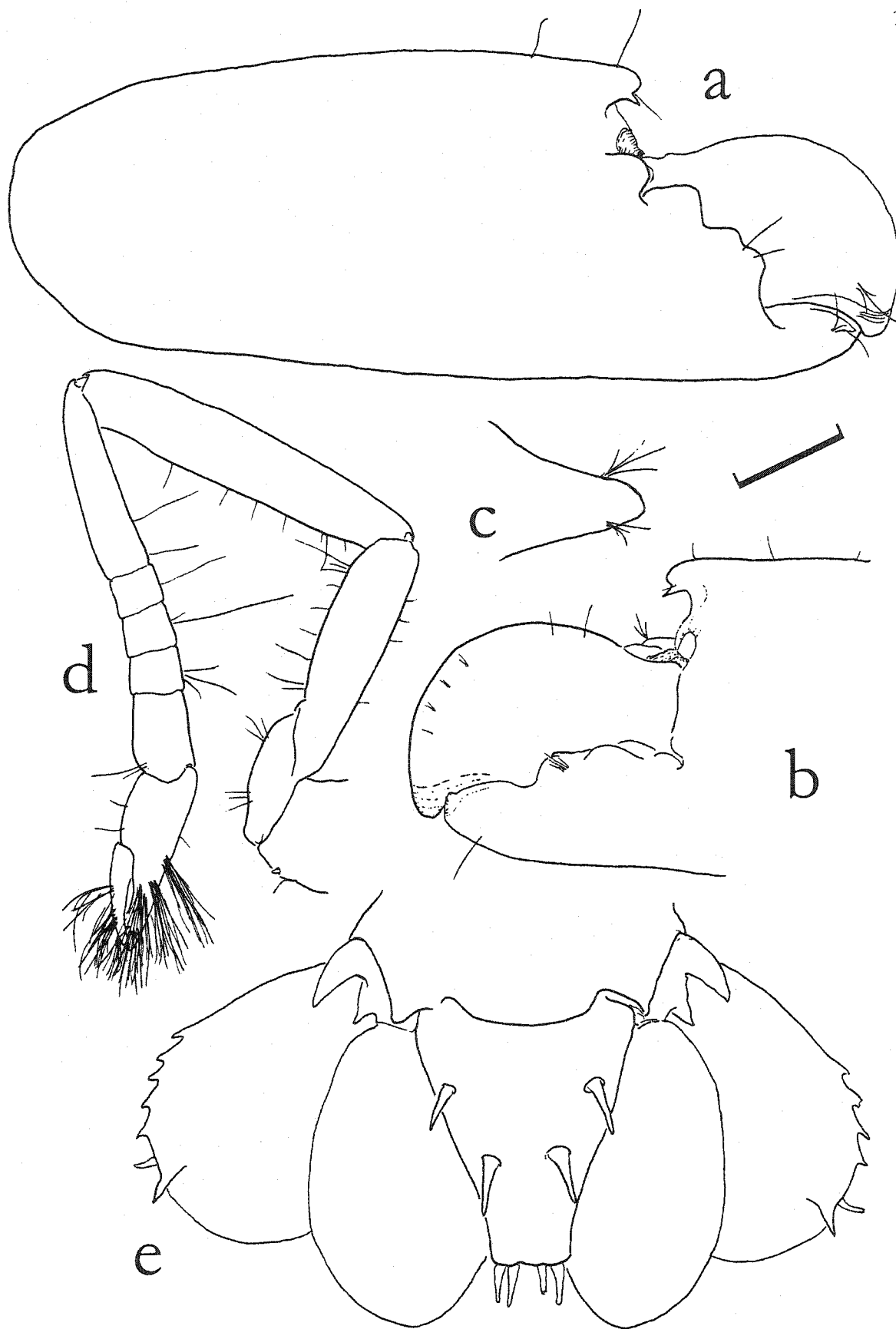


Figure 2-31. *Synalpheus* sp. 6, new species. Paratype male 5.3 mm (USNM 1019057): a, chela of major first pereiopod, lateral view; b, same, detail of distal portion, alternate lateral view; c, same, tip of pollex, ventral view; d, left second pereiopod, lateral view; e, telson and uropods, dorsal view. Scale bar = 1 mm for a, b, 0.7 mm for c, e, and 0.6 for d.





**DESCRIPTION OF HOLOTYPE-** Body form subcylindrical; carapace smooth, with scattered short setae; pterygostomian corner produced into blunt acute angle, and posterior margin with cardiac notch distinct.

Rostrum lanceolate, slightly upturned and laterally compressed; narrower, but about as long as orbital hoods; these latter dorsally convex with flattened mesial slope wider than lateral edge, and converging under base of rostrum; in dorsal view, ocular hoods squarely rounded and blunt anteriorly, margins convex, separated from rostrum by deep adrostral sinus. Ocular processes conspicuously broad. Ocellary beak in lateral view, broad. Stylocerite slender; mesial margin slightly concave; tip acute; reaching nearly as far as distal margin of first antennular peduncle; this latter segment without ventromesial tooth, and with 2 basal ventral processes. Basicerite with dorsolateral corner slightly produced into blunt acute angle; longer ventrolateral spine clearly overreaching tip of stylocerite. Scaphocerite blade totally absent, acute lateral spine robust, with lateral margin slightly concave, barely overreaching antennular peduncle, and reaching slightly shorter than basicerite lateral spine; mesial projection at base of scaphocerite present. Third maxilliped with distal circlet of spines on distal segment, and without ventrodiscal spine on antepenultimate segment; remaining mouthparts as figured.

Major first pereiopod massive, fingers shorter than half the length of palm; pollex somewhat shorter than dactyl; in ventral view, outer face of pollex without any pronounced protuberance. Palm of chela with distal superior margin produced into prominent tubercle with downwardly directed acute spine on its ventral surface. Merus, extensor margin strongly convex, with distal angular projection.

Minor first pereiopod with palm about 2 times longer than high; fingers clearly shorter than palm; dactyl with opposing margin straight, blade-like, with 2 distinct unequal teeth parallel to dactyl axis; transverse dorsal setal combs on dactyl, very conspicuous; pollex with opposing surface obliquely concave, and subdistal accessory bump. Extensor margin of merus convex, ending in right angle.

Second pereiopod with carpus 5-segmented, distinctly longer than merus.

Third pereiopod stout; dactyl biunguiculate, with flexor unguis thicker than extensor; propodus of right leg with row of 8 (left leg with 9) mobile spines on lower margin and one pair on distal end; carpus with one mobile distal spine on flexor margin; merus without spines on flexor margin; mesial lamella on coxa present. Fourth pereiopod similar to third, but weaker. Fifth pereiopod similar to fourth but slender, with 12 parallel rows of transverse setal combs, 3 mobile spines, and 1 distal pair of mobile spines on ventral face of propodus; carpus without distal spine.

First pleura of male with posterior corner distinctly produced ventrally and anteriorly, hook-like; second to fourth pleura of male with lower margin produced into acute angle; fifth pleura similar but more blunt. First pleopod of male, with 8 terminal setae on endopod; second pleopod of male with marginal setae on exopod originating close to base on external margin; appendix interna on second to fifth male pleopods, present. Telson, space between distal spines about one-third of distal margin; marginal convex lobe absent; posterior corners adjacent to spines not produced. Anal flaps absent. Perianal setae absent. Postanal setal brush absent. Uropods with 5 fixed teeth on outer margin of exopod.

**COLOR-** Specimens in life have a dull orange-brown to reddish overall appearance, with the exception of the tips of the major chela which are brown. This latter feature was still

Figure 2-32. *Synalpheus* sp. 6, new species. Paratype male 5.3 mm (USNM 1019057): a, right third pereiopod; b, same, detail of distal portion; c, right fourth pereiopod; d, same, detail of distal portion; e, right fifth pereiopod; f, same, detail of distal portion; g, right first pleopod; h, same, detail of distal portion of endopod; i, right second pleopod. Scale bar = 1 mm for a, c, e, 0.4 mm for b, d, f, 0.8 for g, i, and 2 mm for h.

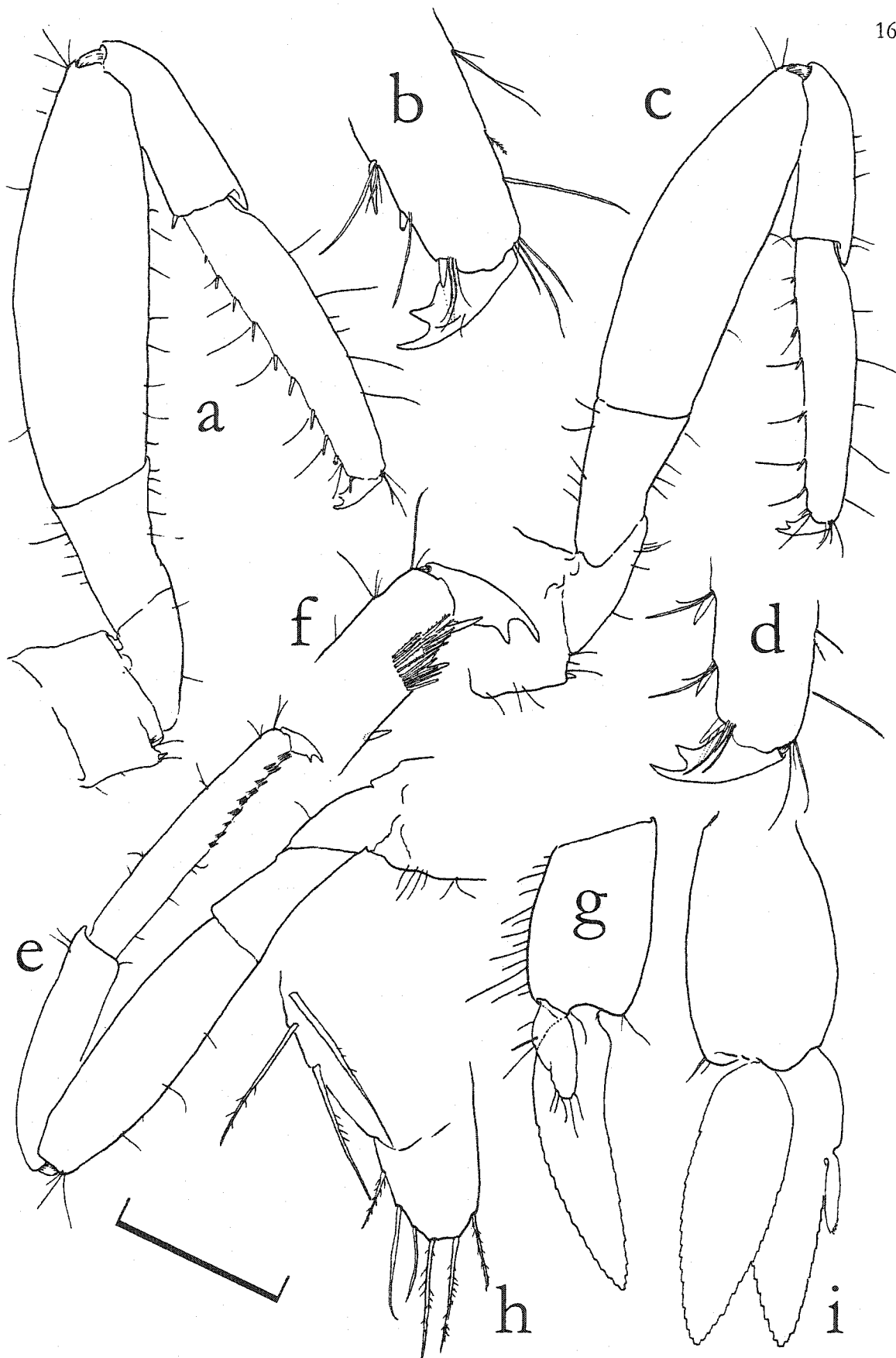
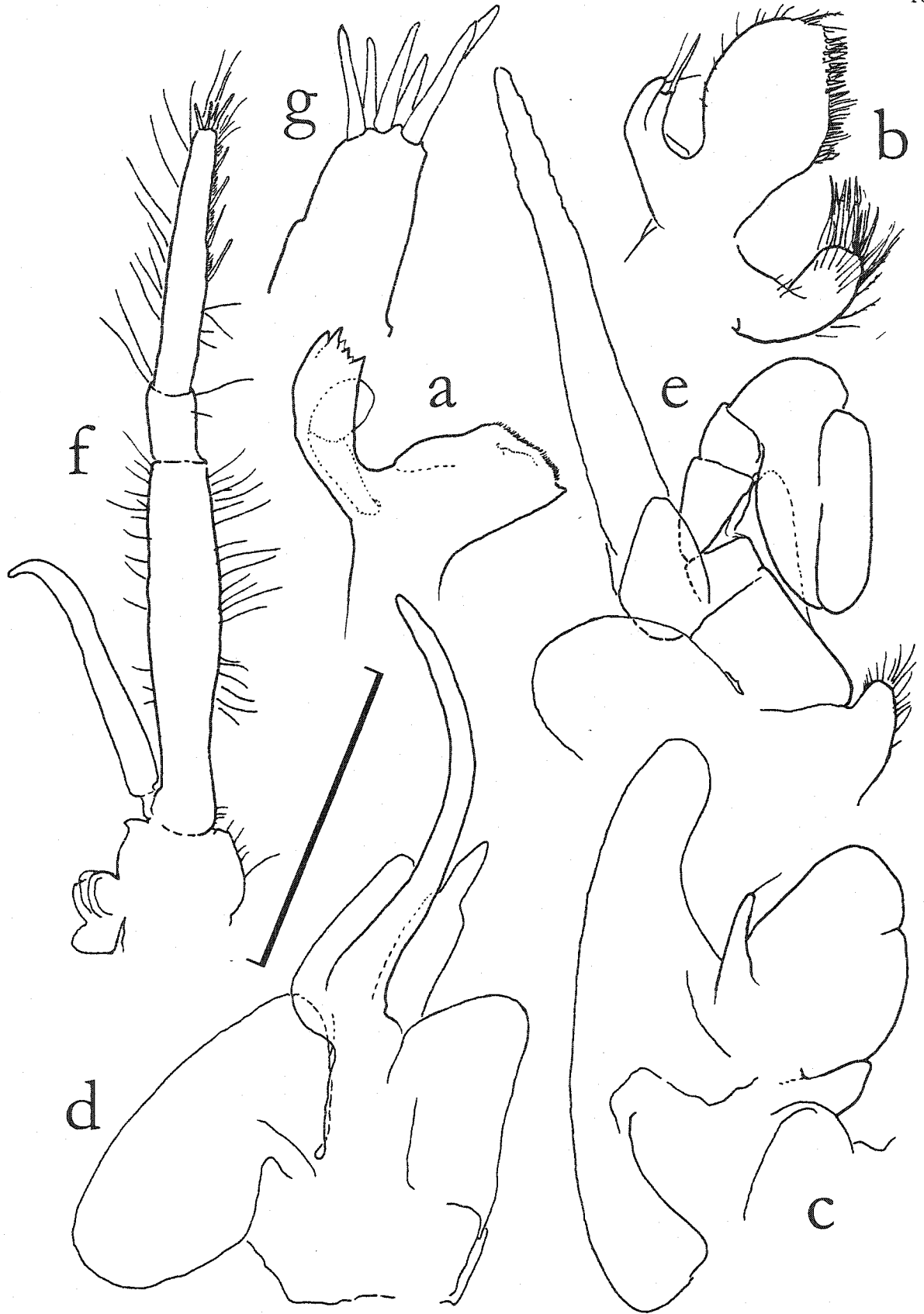


Figure 2-33. *Synalpheus* sp. 6, new species. Mouthparts. Paratype male 5.3 mm (USNM 1019057): a, right mandible; b, right first maxilla; c, right second maxilla; d, right first maxilliped; e, right second maxilliped; f, right third maxilliped; g, same, detail of distal portion, alternate lateral view. Scale bar = 1 mm for a, b, c, d, e, 2 mm for f, and 0.5 mm for g.



evident in some preserved specimens as a translucent fringe. Ovaries and embryos are brick-red.

**ETYMOLOGY-** The future specific name is a Mayan word for "another" or "different" and was chosen to underscore the fact that this is yet another new species of *Synalpheus*.

**VARIATIONS-** *Synalpheus* sp. 6 exhibits the typical sexual dimorphism on the first abdominal pleura, which is broadly rounded only in the female. Also, the number of fixed teeth on the outer margin of the uropodal exopod varies from 4 to 6, rarely 3 or 7, but the most frequent number is 5.

**ECOLOGY-** This species is most frequently found inside the canals of the sponge *Lissodendoryx colombiensis* (and *L. strongylata*?). Other occasional hosts include the midnight blue sponge *Hymeniacidon caerulea*, *Pachypellina podatypa*, and an unidentified yellow sponge.

**DISTRIBUTION-** Western Atlantic: Belize, San Blas Islands, Panama.

**REMARKS-** There is considerable morphological similarity between *S.* sp. 6 and a group of species that includes *S. longicarpus* and *S. pandionis* (Table 2-1). This new species most closely resembles *S.* sp. 5, n.sp., which preferentially inhabits *Hymeniacidon caerulea*. However, *S.* sp. 6 attains larger sizes, never has any trace of a blade on the scaphocerite, and has the second to fourth male pleurae more pointed.

Coutière (1909) erected *Synalpheus grampusi* for a group of specimens that resemble *S.* sp. 6, but after examining the type series I am confident in erecting a new species. In the description of *S. grampusi*, Coutière (1909) recognized several diagnostic characters also present in *S.* sp. 6, most notably the rounded ocular hoods, the shape of the chelae, the fixed teeth on the uropod, and the absence of a blade on the scaphocerite. However, the two largest syntypes (USNM 38399) of *S. grampusi* have a blade on the scaphocerite, which is why



Chace (1972) decided to synonymize it with *S. pandionis* (see remarks under this species).  
Coutière (1909) called “anomalous” the specimen depicted in his figure 36a, and it is this illustration that most strongly resembles both his description of *S. grampusi* and *S. sp. 6*.  
Chace (1972) already suspected that the type series of *S. grampusi* includes a mixture of taxa, and suggested that “a new name might have to be assigned” for *S. grampusi* if proven valid.  
Furthermore, according to Article 72.4.1 of the International Code of Zoological Nomenclature (ICZN 1999), since Coutière (1909) referred to the specimens without blade as “anomalous”, they should not be considered as syntypes. Consequently the only name-bearing specimens are those with a blade, *i. e.* the pair of largest specimens in lot USNM 38399, but the third specimen in the lot ( a smaller ovigerous female without blade) is not a real syntype. Evidently, trying to conserve the name “*Synalpheus grampusi*” does not grant any clarity to the taxonomy of the genus.

### Discussion

After an independent reevaluation of the external morphology of shrimp in the genus *Synalpheus* Bate, 1888, I have now recorded 32 species from Carrie Bow Cay, Belize, six of which were previously unknown to science. I have also resurrected *S. osburni* Schmitt, 1933 from the synonymy of *S. goodei* Coutière, 1909. The material I examined included types of most of the species.

*Synalpheus* is second only to *Alpheus* in number of species within the family Alpheidae. Unlike those in *Alpheus*, the species of *Synalpheus* have a consistent general morphology with only slight, often subtle variations. Despite the small sizes that species of *Synalpheus* attain, and their cryptic habits, these shrimp are among the most abundant crustaceans in coral reef

communities. Furthermore, there are frequent departures from typical forms in most of the species which apparently represent both normal intraspecific variability and even morphological aberrations. Interestingly, some of the variations are sometimes consistent in several or even all of the individuals in a given sponge, suggesting a hereditary basis within the often closely related shrimps therein (Duffy 1996a, 1996c). Dardeau (1984) also acknowledged these two kinds of variation. He briefly speculated on the possible genetic and evolutionary causes, alluding to the lack of knowledge on the biology of *Synalpheus*. A better perception of the intraspecific variability within this genus should include a refined distinction within what might be called normal variation. Sexual dimorphism, which is still not fully understood, and some characters that appear to be related to size, ultimately could be dependent on age. For example, the extreme modification of the largest queens in *S. filidigitus*, where the major chela is transformed into a second symmetrical minor chela, is probably also influenced by social circumstances inside the colony. Duffy and Macdonald (1999) suggested that a plausible explanation for this transformation would be that the queen gets rid of the energetic burden resulting from the maintenance of a huge chela, because once they have reached a certain size they no longer need to reinforce the exclusivity of their reproductive status. Duffy and Macdonald (1999) concluded that royal status could be maintained by other members of the colony as in certain social insects. Finally, caution has to be exerted also with specimens undergoing regeneration of appendages due to traumatic alterations or due to parasitism.

Regarding the ensemble of western Atlantic species in particular, most of the *Synalpheus* species are sponge-dwellers, and this habitat poses logistic problems to the naturalist, which, however, can be partially resolved by two frequently neglected features, that in this study

proved to be most informative, *i. e.*, microhabitat data and observations on live specimens. That is, given the generally strong host specificity, a positive identification of the host sponge usually hints at the identity of the shrimp. Furthermore, color patterns of live shrimp often differ quite distinctively between morphologically similar species (*vide* Color Plates), and thus often provide the first clues of the identity of several species.

All of the previously mentioned features of *Synalpheus* have been poorly understood in the past, and contributed to taxonomic confusion. An outstanding example of the disarray within this taxon is the case of *S. longicarpus*, the whereabouts of whose holotype is unknown. This is one of the earliest described and largest species, occupying very common sponges, and probably widely distributed. However, the most useful distinguishing characters for this species have not previously been recognized, namely the subsiding cardiac notch on the carapace, the slender orbital hoods, the shape of the major chela, and the feeble spines on the dorsal surface of the telson (Table 2-1). By considering these and other characters, the resurrection of *S. pandionis* as asserted by Dardeau (1984) now has been substantiated, and three related new species in this complex have been discovered in Carrie Bow Cay, plus one in Panama (Chapter 3).

It is almost 20 years since Dardeau (1984) contributed to the knowledge of the Gambarelloides group, but the taxonomy of western Atlantic *Synalpheus* is still far from settled. As specifically suggested both by Banner and Banner (1975) and by Dardeau (1984), detailed information on microhabitat through conscientious fine-scale sampling has greatly contributed in separating the species in the genus *Synalpheus*. Thus, my revised taxonomy should greatly aid further studies on the ecology, evolution, and behavior of this fascinating but poorly understood group of animals.

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**Key to the Gambarelloides group of  
species of *Synalpheus* from the western Atlantic.**

1. Transverse dorsal setal combs on dactyl of minor first pereiopod, absent (Coxal lamella on third pereiopod, absent) ..... Non Gambarelloides
- Transverse dorsal setal combs on dactyl of minor first pereiopod, present ..... 2
- 2(1). First segment of antennular peduncle with ventromesial tooth ..... 3
- First segment of antennular peduncle without ventromesial tooth ..... 4
- 3(2). Pollex of major first pereiopod with conspicuous basal protuberance, best seen on a ventral view ..... *Synalpheus sanctithomae*
- Pollex of major first pereiopod without basal protuberance ..... *Synalpheus mcclendonii*
- 4(2). Basicerite with dorsolateral corner acute, or even with sharp spine ..... 5
- Basicerite with dorsolateral corner straight or obtuse ..... 12
- 5(4). Pollex of major first pereiopod with conspicuous basal protuberance, best seen on a ventral view ..... *Synalpheus williamsi*
- Pollex of major first pereiopod without conspicuous basal protuberance ..... 6
- 6(5). Second pereiopod with carpus 4-segmented ..... 7
- Second pereiopod with carpus 5-segmented ..... 10
- 7(6). Palm of chela with distal superior margin flared into conical tubercle (without accessory spine) ..... *Synalpheus rathbunae*
- Palm of chela with distal superior margin inflated into blunt projection (normally with small accessory spine) ..... 8

- 8(7). Rostrum triangular, broad basally; 1<sup>st</sup> pleura of male, anterior corner broadly obtuse, posterior corner with thick hook ..... *Synalpheus filidigitus*
- Rostrum lanceolate, narrow basally; 1<sup>st</sup> pleura of male, anterior corner acute, posterior corner with slender hook ..... 9
- 9(8). Scaphocerite spine distinctly overreaching antennular peduncle; 2<sup>nd</sup> to 5<sup>th</sup> pleura of male strongly acuminate ..... *Synalpheus* sp. 2
- Scaphocerite spine not overreaching antennular peduncle; 2<sup>nd</sup> to 5<sup>th</sup> pleura of male not acuminate ..... *Synalpheus regalis*
- 10(6). Scaphocerite with narrow blade present; dactyl of minor first pereiopod with two strong subdistal accessory teeth; uropodal exopod with internal fixed tooth clearly thicker than mobile spine ..... *Synalpheus goodei*
- Scaphocerite without any trace of a blade; dactyl of minor first pereiopod with two subdistal accessory cants; uropodal exopod with internal fixed tooth not much thicker than mobile spine ..... 11
- 11(10). Rostrum elongate clearly overreaching base of stylocerite, much longer than orbital teeth; palm of minor first pereiopod with distinct spine overhanging base of dactyl; uropodal exopod with 8 fixed teeth on external margin ..... *Synalpheus osburni*
- Rostrum barely reaching base of stylocerite, slightly longer than orbital teeth; palm of minor first pereiopod without spine overhanging base of dactyl; uropods with 2 fixed teeth on external margin of exopod ..... *Synalpheus* sp. 4

- 12(4). Third pereiopod with carpus and merus with lateral flanges forming a cavity when meeting together ..... *Synalpheus androsi*
- Third pereiopod with carpus and merus without lateral flanges forming a cavity when meeting together ..... 13
- 13(12). Dactyl of minor first pereiopod with 3 subequal strong teeth on distal margin arranged parallel to plane of dactyl (major first pereiopod with pollex greatly reduced and superior border of palm tapering upwardly into acute spine) ..... *Synalpheus pectiniger*
- Dactyl of minor pereiopod without 3 distal teeth parallel to plane of dactyl ..... 14
- 14(13). Dactyl of minor first pereiopod excavate on ventral side giving it the appearance of a spoon; with two strong subequal teeth and a straight cant arranged perpendicularly to the plane of dactyl ..... *Synalpheus paranepetunus*
- Dactyl of minor first pereiopod not excavate, nor spoon-shaped ..... 15
- 15(14). Rostrum minuscule (triangular), separated from broadly obtuse ocular hoods by shallow and wide sinus ..... *Synalpheus brevifrons*
- Rostrum not minuscule, separated from ocular hoods by deep sinus ..... 16
- 16(15). Scaphocerite clearly overreaching antennular peduncle ..... *Synalpheus anasimus*
- Scaphocerite not overreaching antennular peduncle ..... 17
- 17(16). Tip of third maxilliped without spines, only setae ..... *Synalpheus barahonensis*
- Tip of third maxilliped with circlet of strong spines besides setae ..... 18
- 18(17). Cardiac notch reduced due to strongly obtuse superior angle .... *Synalpheus longicarpus*
- Cardiac notch normal, with superior angle not strongly obtuse ..... 19
- 19(18). Major first pereiopod, pollex less than half as long as dactyl ... *Synalpheus disparodigitus*
- Major first pereiopod, pollex not reduced to less than half the length of dactyl ..... 20

- 20(19). Palm of major first pereiopod with distal superior margin produced into tapering acute spine or blunt tubercle, but without accessory sharp spine; ocular hoods triangular . . . . . 21
- Palm of major first pereiopod with distal superior margin produced into blunt tubercle with accessory sharp spine; ocular hoods not triangular . . . . . 27
- 21(20). Palm of major first pereiopod with distal superior margin produced into blunt process, seldom barely discernible; brush of setae on dorsal surface of dactyl of minor chela arranged in two distinct longitudinal series . . . . . *Synalpheus chacei*
- Palm of major first pereiopod with distal superior margin produced into acute process, not always sharp; brush of setae on dorsal surface of dactyl of minor chela not arranged in two distinct longitudinal series . . . . . 22
- 22(21). Palm of major first pereiopod with distal superior margin produced into acute conic protuberance, distinctly oriented obliquely upward . . . . . *Synalpheus brooksi*
- Palm of major first pereiopod with distal superior margin produced into acute process, not conic, distinctly oriented anteriorly or ventrally . . . . . 23
- 23(22). Dactyl of minor first chela obscurely bidentate . . . . . *Synalpheus agelas*
- Dactyl of minor first chela deeply bidentate . . . . . 24
- 24(23). Major first pereiopod, merus with flat distal angular projection on external margin; 3<sup>rd</sup> and 4<sup>th</sup> abdominal pleura of male with a distinct concavity on lower margin, producing the appearance of a broad "W" . . . . . *Synalpheus herricki*
- Major first pereiopod, merus without angular projection; 3<sup>rd</sup> and 4<sup>th</sup> abdominal pleura of male with lower margin broadly rounded to obtuse . . . . . 25
- 25(24). Major first pereiopod, palm terminating dorsodistally in blunt spine directed distoventrally; minor first pereiopod, carpus about half as chela . . . . . *Synalpheus bousfieldi*

- Major first pereopod, palm terminating dorsodistally in blunt spine not directed distoventrally; minor first pereopod, carpus longer than half length of chela ..... 26
- 26(25). Shallow adrostral sinuses; telson with anterior pair of spines on dorsal surface arising in posterior half ..... *Synalpheus heardi*
- Deep adrostral sinuses; telson with anterior pair of spines on dorsal surface not arising in posterior half ..... *Synalpheus* sp. 3
- 27(20). Dactyl of minor first pereopod strongly bidentate with subequal teeth; ocular hoods slender with lateral margin convex, and submesial straight to convex ..... 28
- Dactyl of minor first pereopod bidentate with obscure accessory subdistal tooth; ocular hoods broadly squared, with distal margin strongly convex ..... 29
- 28(27). Scaphocerite without blade; strong projection under base of rostrum; inner submesial fixed tooth on uropodal exopod in-set, producing a lobe between that tooth and the mobile spine ..... *Synalpheus rufus*
- Scaphocerite with blade reduced; base of rostrum without strong projection; inner submesial fixed tooth on uropodal exopod laying next to mobile spine, without a lobe between the two of them ..... *Synalpheus* sp. 1
- 29(27). Inner submesial fixed tooth on uropodal exopod in-set, producing a lobe between that tooth and the mobile spine; pollex of major first pereopod with conspicuous basal protuberance, best seen on a ventral view ..... *Synalpheus pandionis*
- Inner submesial fixed tooth on uropodal exopod laying next to mobile spine, without a lobe between the two of them; pollex of major first pereopod without conspicuous basal protuberance ..... 30

- 30(29). Scaphocerite with blade reduced; lateral spines on distal margin of telson distinctly shorter  
and slightly thicker than submesial ..... *Synalpheus* sp. 5
- Scaphocerite without blade; spines on distal margin of telson, subequal . . . *Synalpheus* sp. 6



Table 2-1.- Morphological characters useful in distinguishing six closely related species of *Synalpheus*.

	orbital hoods	orbitorostral process	cardiac notch	ocular process	stylocerite	scaphocerite blade	small p1 distal spines on dactylus	posterior corner 2 <sup>nd</sup> pleura in ♂	inner submesial fixed tooth on exopod of uropod	distal spines of telson	spines on dorsal face of telson	protuberance at base of pollex
new sp. 1	hoof	absent	normal	long	slender	reduced	subequal	acute	on edge	unequal	strong	obtuse
<i>longicarpus</i>	slender	absent	reduced *	broad	slender	reduced	subequal	acute	on edge	unequal	feeble	obtuse
<i>pandionis</i>	broad	absent	normal	double	slender	reduced	unequal	acute	in-set	subequal	strong	acute
new sp. 7	hoof	deep	normal	broad	slender	absent	subequal	acute	in-set	un/sub	strong	obtuse
new sp. 5	broad	simple	normal	broad	thick	reduced	unequal	obtuse	on edge	unequal	strong	absent
new sp. 6	broad	absent	normal	broad	slender	absent	unequal	obtuse	on edge	subequal	strong	absent

\* upper angle of notch remarkably obtuse

Table 2-2. Morphological characters useful in distinguishing four closely related species of *Synalpheus*.

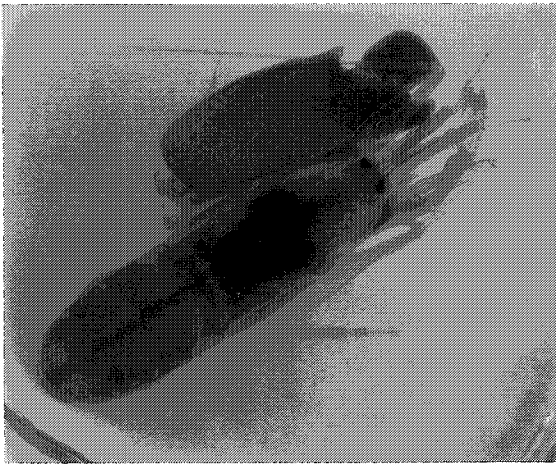
	Major chela, anterior-most edge of palm	Dactyl of the minor chela	Posterior corner of 1 <sup>st</sup> pleura in males	2 <sup>nd</sup> pleura in males
<i>S. sp. 2</i>	inflated + spine	simple	long, hooked	acute point
<i>S. filidigitus</i>	inflated + spine	with accessory spine	short, hooked	widely obtuse
<i>S. rathbunae</i>	flared, no spine	simple	long, acute	acute point
<i>S. regalis</i>	inflated (+ spine)	simple	long, hooked	thick point

Table 2-3. List of species of *Synalpheus* recorded from the western Atlantic.

\* indicates that the species is not present in collections from Carrie Bow Cay.

GAMBARELLOIDES GROUP	NON GAMBARELLOIDES
<i>Synalpheus agelas</i> Pequegnat and Heard, 1979	<i>Synalpheus apioceros</i> Coutière, 1909
<i>Synalpheus androsi</i> Coutière, 1909	<i>Synalpheus brevicarpus</i> Coutière, 1909
<i>Synalpheus boussfieldi</i> Chace, 1972	<i>Synalpheus dominicensis</i> Armstrong, 1949
<i>Synalpheus brevifrons</i> Chace, 1972	<i>Synalpheus fritzmuelleri</i> Coutière, 1909
<i>Synalpheus brooksi</i> Coutière, 1909	<i>Synalpheus hemphilli</i> Coutière, 1908
<i>Synalpheus chacei</i> Duffy, 1998	<i>Synalpheus minus</i> (Say, 1818)
<i>Synalpheus filidigitus</i> Armstrong, 1949	<i>Synalpheus obtusifrons</i> Chace, 1972
<i>Synalpheus goodei</i> Coutière, 1909	<i>Synalpheus scaphoceros</i> Coutière, 1910
<i>Synalpheus herricki</i> Coutière, 1909	<i>Synalpheus townsendi</i> Coutière, 1909
<i>Synalpheus longicarpus</i> (Herrick, 1891)	* <i>Synalpheus curacaoensis</i> Schmitt, 1924
<i>Synalpheus mclendonii</i> Coutière, 1910	
<i>Synalpheus pandionis</i> Coutière, 1909	
<i>Synalpheus paranephtunus</i> Coutière, 1909	
<i>Synalpheus pectiniger</i> Coutière, 1907	
<i>Synalpheus regalis</i> Duffy, 1996	
<i>Synalpheus sanctithomae</i> Coutière, 1909	
<i>Synalpheus williamsi</i> Ríos and Duffy, 1999	
<i>Synalpheus</i> sp. 1, new species	
<i>Synalpheus</i> sp. 2, new species	
<i>Synalpheus</i> sp. 3, new species	
<i>Synalpheus</i> sp. 4, new species	
<i>Synalpheus</i> sp. 5, new species	
<i>Synalpheus</i> sp. 6, new species	
<i>Synalpheus</i> sp. 7, new species	
* <i>Synalpheus anasimus</i> Chace, 1972	
* <i>Synalpheus barahonensis</i> Armstrong, 1949	
* <i>Synalpheus disparodigitus</i> Armstrong, 1949	
* <i>Synalpheus heardi</i> Dardeau, 1984	
* <i>Synalpheus osburni</i> Schmitt, 1933	
* <i>Synalpheus rathbunae</i> Coutière, 1909	

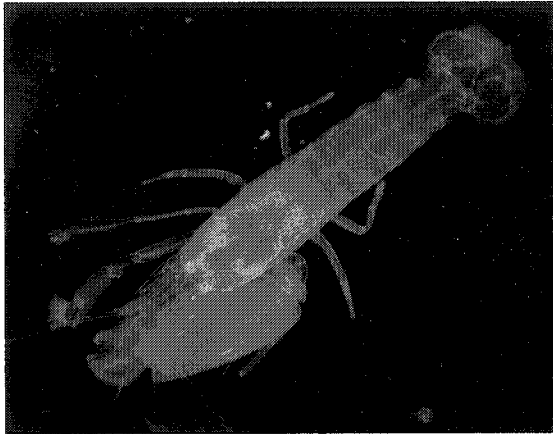
Plate I



*Synalpheus* sp. 1 male



*Synalpheus* sp. 1 female



*Synalpheus* sp. 5 male



*Synalpheus* sp. 5 female

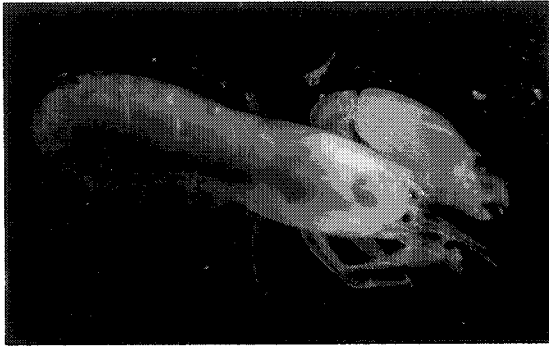


*Synalpheus williamsi* female

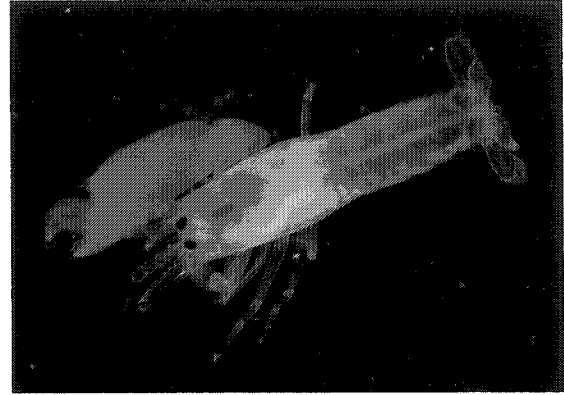


*Synalpheus williamsi* male

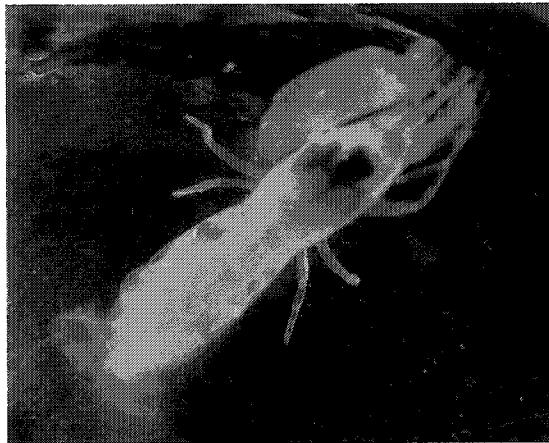
Plate II



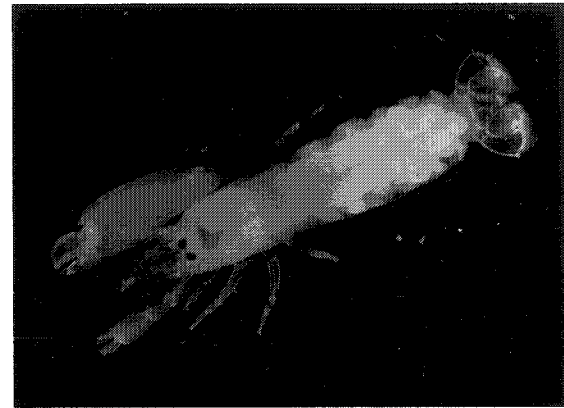
*Synalpheus* sp. 3 female



*Synalpheus* sp. 3 male



*Synalpheus agelas* female



*Synalpheus paraneptunus* female

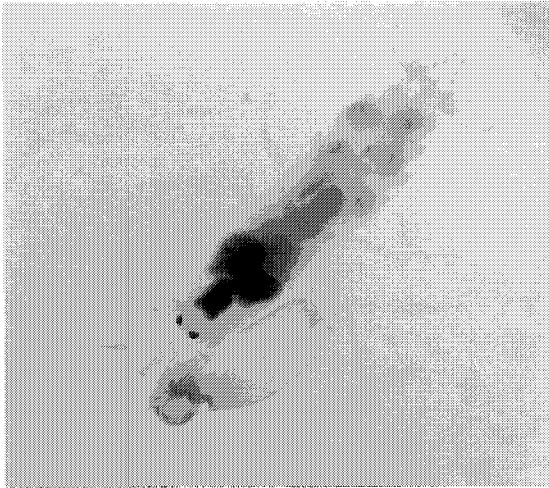


*Synalpheus chacei* female

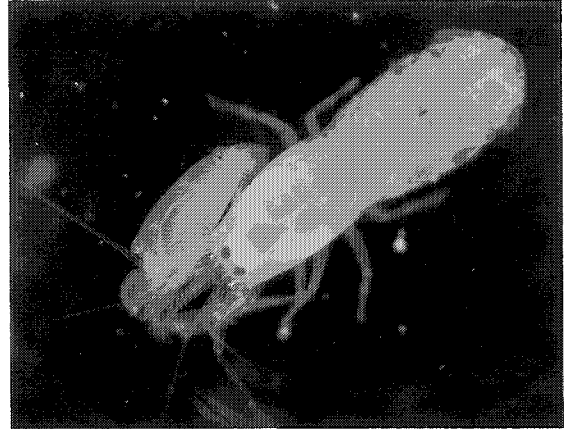


*Synalpheus filidigitus* female

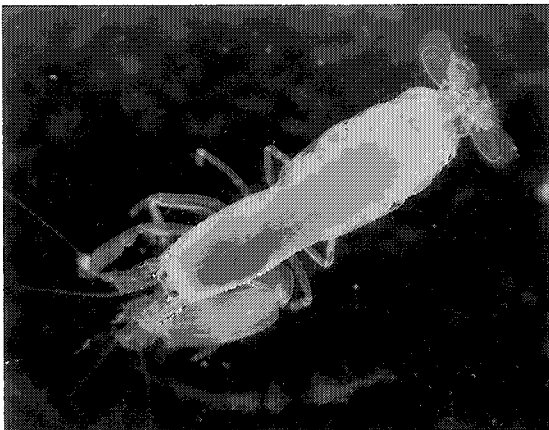
Plate III



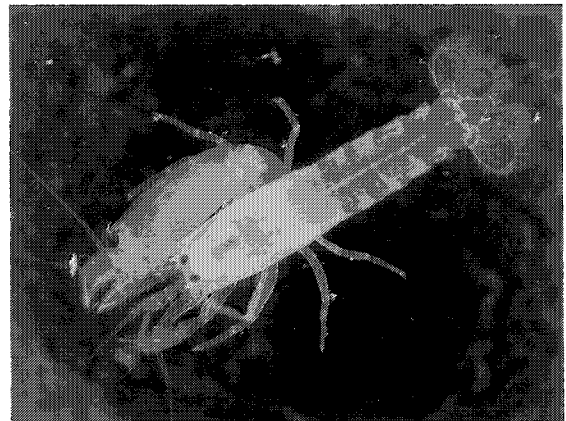
*Synalpheus androsi* female



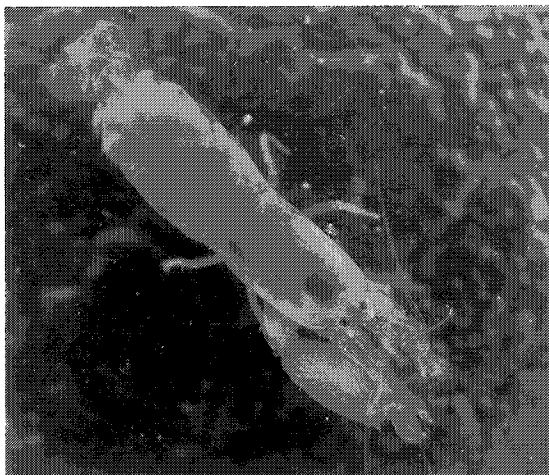
*Synalpheus brevifrons* female



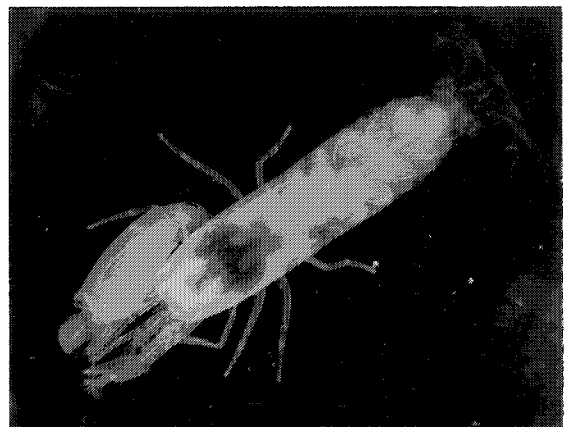
*Synalpheus bousfieldi* female



*Synalpheus bousfieldi* male



*Synalpheus* sp. 2 female

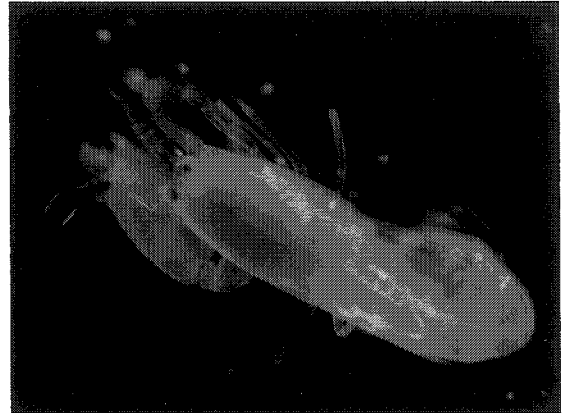


*Synalpheus* sp. 4 female

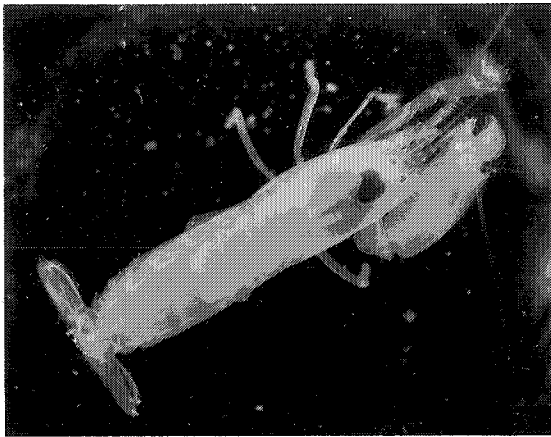
Plate IV



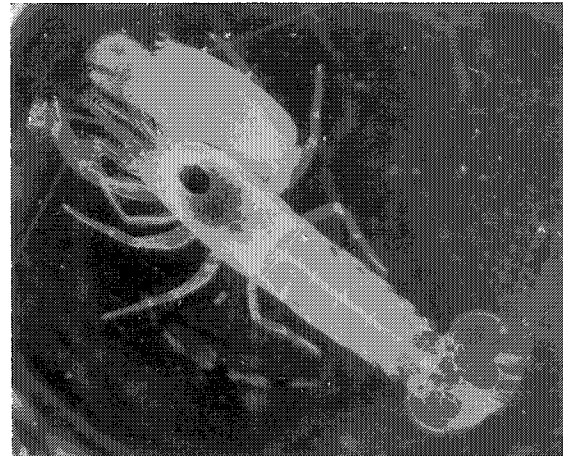
*Synalpheus pandionis* female



*Synalpheus sanctithomae* female



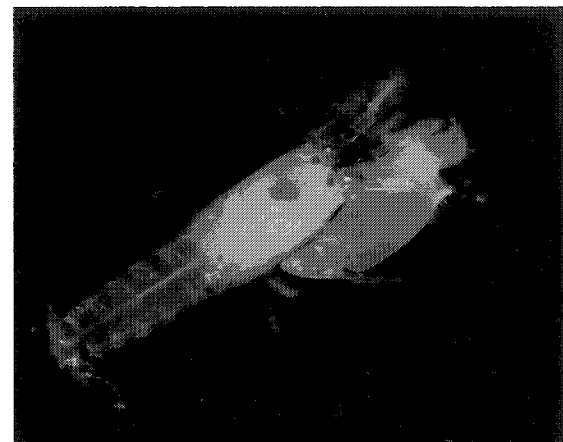
*Synalpheus goodei* female



*Synalpheus goodei* male



*Synalpheus regalis* female



*Synalpheus regalis* male

## CHAPTER THREE

### Description of a new species of sponge-dwelling shrimp

#### from the Atlantic coast of Panama

#### (Crustacea: Decapoda: Alpheidae: *Synalpheus*).

**Abstract-** A new species of *Synalpheus* Bate, 1888 is described based on specimens collected inside the loggerhead sponge *Sphaciospongia vesparium* (Lamarck) from the Atlantic coast of Panamá. The new species is most similar morphologically to *S. pandionis* Coutière, 1909, but the two species are consistently different in several morphological features, and occupy distinct species of sponges. The two species can be separated based on shape of the ocular hoods, scale on the scaphocerite, and shape of the pollex of the major first pereiopod.

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The snapping shrimp in the genus *Synalpheus* Bate, 1888 are abundant in shallow tropical reef habitats worldwide and have a similar general appearance. Most of the species known from the western Atlantic belong in the Gambarelloides group (Coutière 1908, 1909, Dardeau 1984) and live as internal parasites or commensals of coral-reef sponges (Duffy 2003). Among the dwellers in the loggerhead sponge *Sphaciospongia vesparium* in Atlantic Panama, we collected a previously undescribed species. It belongs in a clade that includes *S. pandionis*, *S. goodei*, *S. longicarpus* and three additional undescribed species (Morrison, Ríos and Duffy, in press, Chapter 2). In addition to its strikingly different color pattern, the new species can be distinguished by



a combination of several morphological characters, including the ocular hoods, the scale on the scaphocerite, and the shape of the pollex of the major first pereopod. Observations on the first larval stage obtained in captivity indicate that it is an early swimming zoea, rather than a megalopa.

Type material has been deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D. C. (USNM). Measurements indicated are of carapace length including rostrum.

### *Synalpheus* sp. 7, new species

Figures 3-1 through 3-4

**TYPE SPECIMENS-** Holotype male, 4.3 mm (USNM 1019059), allotype ovigerous female, 5.2 mm (USNM 1019060), Aguadargana Reef, San Blas Islands, Panama 20 September 1993, from loggerhead sponge, *Sphaciospongia vesparium*, 10 m deep. Additional non paratype material in the VIMS collection: 13 males (3.2 - 5.7 mm); six ovigerous females (4.4 - 5.2 mm).

**DESCRIPTION OF HOLOTYPE-** Body subcylindrical; carapace smooth, glabrous, with pterygostomian corner produced into bluntly acute angle, and posterior margin with cardiac notch distinct. Rostrum lanceolate, about as long as orbital teeth, but clearly narrower, laterally compressed and prolonged postero-ventrally into pyramid shorter than eyes, triangular in frontal view. Ocular hoods dorsally convex; in dorsal view, acute, mesial margins straight to slightly sinuous, separated from rostrum by deep adrostral sinus, outer margins convex.

Stylocerite slender; tip acute; mesial margin slightly concave or straight; distinctly shorter than distal margin of first segment of antennular peduncle; this latter segment without

ventromesial tooth, and with 2 basal ventral processes. Basicerite without spine on dorsolateral corner, and with longer ventrolateral spine clearly overreaching tip of stylocerite. Scaphocerite blade absent (on right side, vestigial); robust, acute lateral spine with lateral margin slightly concave, not overreaching antennular peduncle; reaching as far as basicerite lateral spine. Mesial projection at base of scaphocerite present. Third maxilliped with distal cirlet of spines on distal segment, and without ventrodiscal spine on antepenultimate segment. Other mouthparts as figured.

Major first pereiopod massive, fingers clearly shorter than half length of palm; pollex reduced, noticeably shorter than dactyl; in ventral view, outer face of pollex with an obtuse basal protuberance. Palm of chela with distal superior margin produced into prominent tubercle overhanging small acute spine; merus, with flat angular projection on extensor margin.

Minor first pereiopod with palm about 2 times longer than high; fingers clearly shorter than palm; dactyl with opposing margin straight, blade-like, with 2 strong distal teeth, subequal in length, and parallel to dactyl axis; transverse dorsal setal combs on dactyl, very conspicuous; pollex with margin straight, blade-like, and 2 strong teeth subequal in length; extensor margin of merus sloping smoothly into articulation.

Second pereiopod with carpus 5-segmented, longer than merus.

Third pereiopod slender; dactyl biunguiculate, with clearly unequal unguis; flexor unguis wider at base than extensor; propodus 5.3 times longer than wide, flexor margin with a longitudinal series of 9 slender movable spines and one terminal pair of movable spines flanking base of dactyl; carpus 3.6 times longer than wide, extensor distal margin projected over propodus, slender movable spine on distal flexor margin; merus 4 times longer than wide, without movable spines on flexor margin; ischium unarmed; mesial lamella on coxa present.

Fourth pereopod very similar to third, but weaker. Fifth pereopod more slender than fourth; propodus bearing only 3 movable spines on flexor margin, and 7 transverse rows of thick setae on distal half of posterior face; carpus without spine.

First pleura of male with posterior corner distinctly hook-like; second to fifth pleura of male produced postero-ventrally into acute angle; sixth abdominal segment with acute projection on posteroventral margin, shallow curved inferior concavity, triangular lateral lobe with convex sides, shallow obtuse upper emargination, and convex dorsal margin slightly overhanging telson. Female first to fourth pleura broadly rounded; fifth pleura with inferior margin concave and posterior corner obtuse. First pleopod of male, with few terminal setae on endopod; second pleopod of male with marginal setae on exopod originating close to base; appendix interna on second to fifth pleopods, present both in female and male. Telson, space between distal spines equal or less than one-third of distal margin; marginal convex lobe absent. Uropods with 4 fixed teeth on outer margin of left exopod, and 3 on right one; mobile spine widely separated both from first adjacent tooth and from much stronger mesial fixed tooth; this latter clearly overlapping disto-lateral corner of exopod, and inwardly removed from emerging point of first fixed tooth.

**COLOR-** Live specimens were bright red due to prominent chromatophores against transparent background all over, except on postocular ovals and branchial area. Sparser distribution of chromatophores near the anterior margin of each abdominal segment gave a banded appearance to some specimens. Chelae same red, with golden fingertips. Some preserved specimens show traces of intense pink coloration on fingertips and spines of telson.

**FIRST LARVA-** Zoeae were obtained from a wild ovigerous female; they have uncovered triangular eyes, lack any traces of pleopods, have the sixth abdominal segment still fused with

the telson, and the uropods are visible inside the telson.

**ETYMOLOGY-** From the Latin word for "red", the specific name will allude to the striking coloration of this shrimp in life. When a piece of loggerhead sponge is split apart, individuals of *S. sp. 7* are readily distinguishable from the more abundant *S. longicarpus*, by their red coloration.

**VARIATIONS-** The process under the rostrum is somewhat longer in some specimens; in a large (5.1 mm) ovigerous female it reaches the ventral margin of the eyes and it has a slight bifurcation on the posterior margin of the tip. In some specimens the ocular hoods look wider than in the holotype. Among all the specimens examined, the scaphocerite on the right side of the holotype is the only one with a very small vestige of a blade. One male (5.3 mm) has the spines of the dactyl on the minor chela noticeably enlarged, and has the anterior corner of the first abdominal pleura acutely pointed. The number of teeth on the outer margin of the uropodal exopod is usually 4 or 5, rarely 6 or 7.

**ECOLOGY-** This shrimp lives inside the loggerhead sponge, *Sphaciospongia vesparium*, usually as adult heterosexual pairs, and one or a few pairs in the same sponge.

**DISTRIBUTION-** Western Atlantic: Bahamas and Panama.

**REMARKS-** This new species of *Synalpheus* belongs in a group of species that include *S. longicarpus*, *S. pandionis*, *S. sp. 1*, *S. sp. 6*, and *S. sp. 5*. It is probably more closely related to *S. pandionis*, but the broader ocular hoods, the large scale on the scaphocerite, and the conspicuous protuberance on the pollex of the major first pereopod in *S. pandionis* allow for a positive separation of the two species (Table 2-1).

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Figure 3-1. *Synalpheus* sp. 7, new species. Paratype male 4.7mm (VIMS 93P0903): a, anterior region of carapace, frontal view; b, same, dorsolateral view; c, detail of left uropod, dorsal view. Holotype male 4.3 mm (USNM 1019059): d, telson and uropods, dorsal view; e, pollex of major first pereiopod, ventral view. Allotype ovigerous female 5.2 mm (USNM 1019060): f, anterior region of carapace and cephalic appendages, lateral view; g, same, dorsal view. Ovigerous female 4.7 mm: h, detail of distal portion of minor first pereiopod, lateral view. Scale bar = 1.0 mm for a, b, d, e, f, g, and 0.5 mm for c, h.

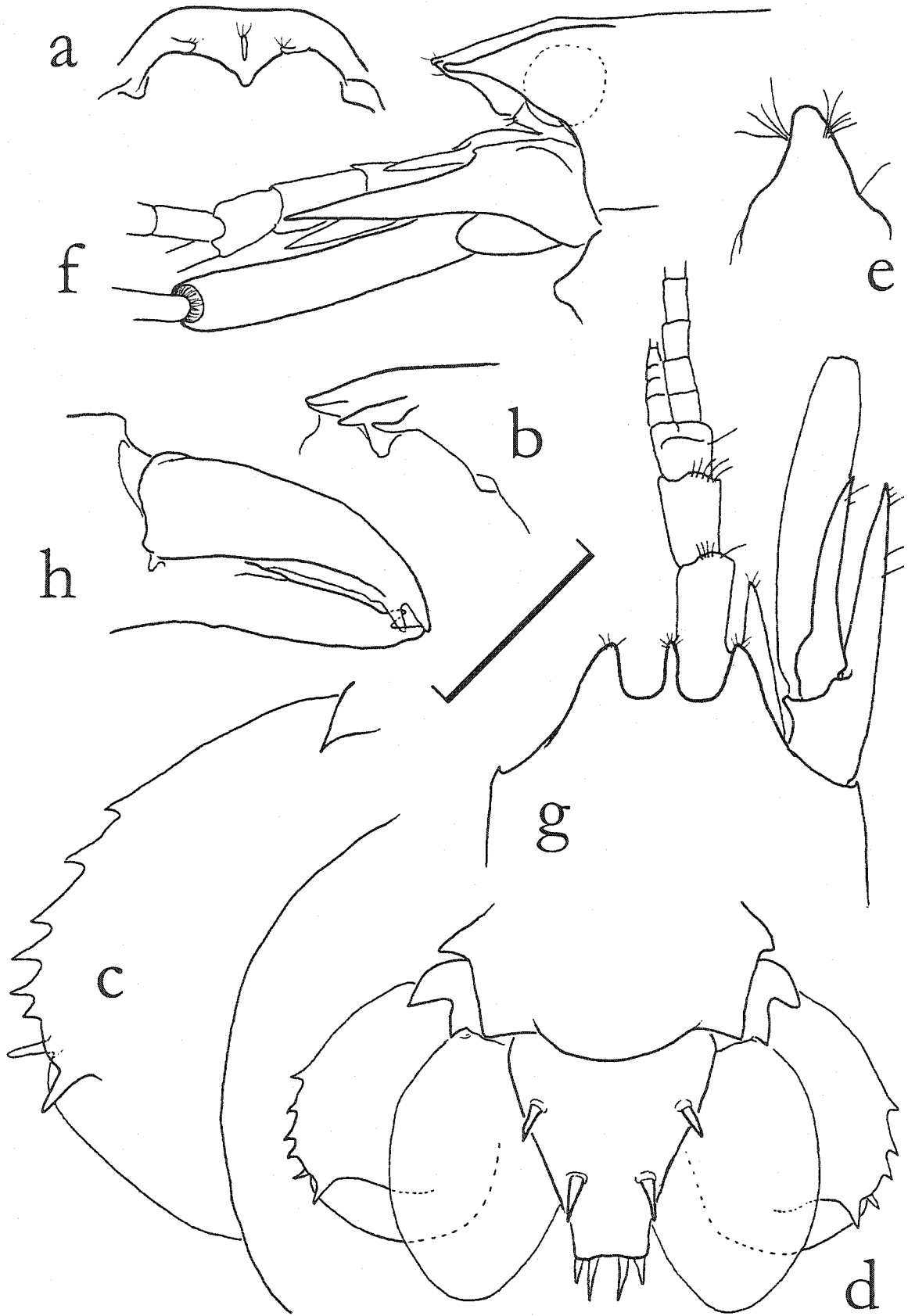


Fig. 3-2. *Synalpheus* sp. 7, new species. Ovigerous female 4.7 mm: a, abdomen with one egg, lateral view. Allotype ovigerous female 5.2 mm (USNM 1019060): b, right first pleopod; c, second pleopod. Paratype male 4.7 mm (VIMS 93P0903): d, left first pleopod; e, second pleopod. Holotype male 4.3 mm (USNM 1019059): f, abdomen, lateral view. Scale bar = 1.0 mm for a, c, f, and 0.5 mm for b, d, e.



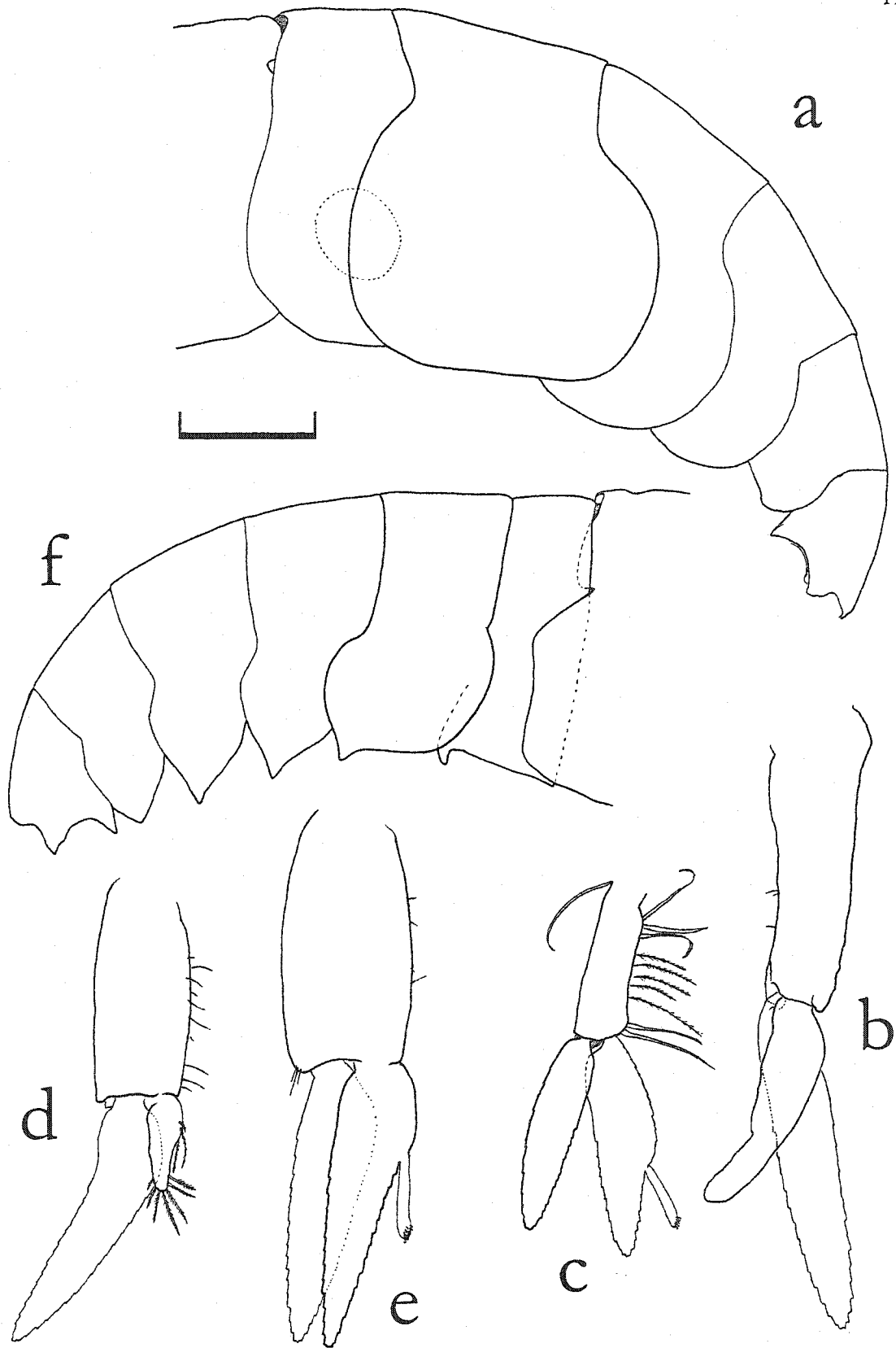


Fig. 3-3. *Synalpheus* sp. 7, new species. Holotype male 4.3 mm (USNM 1019059): a, major first pereiopod, lateral view. Allotype ovigerous female 5.2 mm (USNM 1019060): b, minor first pereiopod, lateral view; c, same, detail of distal portion, lateral view (transverse setal combs omitted). Paratype male 4.7mm (VIMS 93P0903): d, second pereiopod, lateral view; e, third pereiopod, lateral view; f, same, detail of distal portion; g, fourth pereiopod, lateral view; h, same, detail of distal portion; i, fifth pereiopod, lateral view; j, same, detail of distal portion; k, third maxilliped, detail of tip. Scale bar = 1 mm for a, b, d, e, g, i, 0.5 mm for c, and 0.2 mm for f, h, j, k.

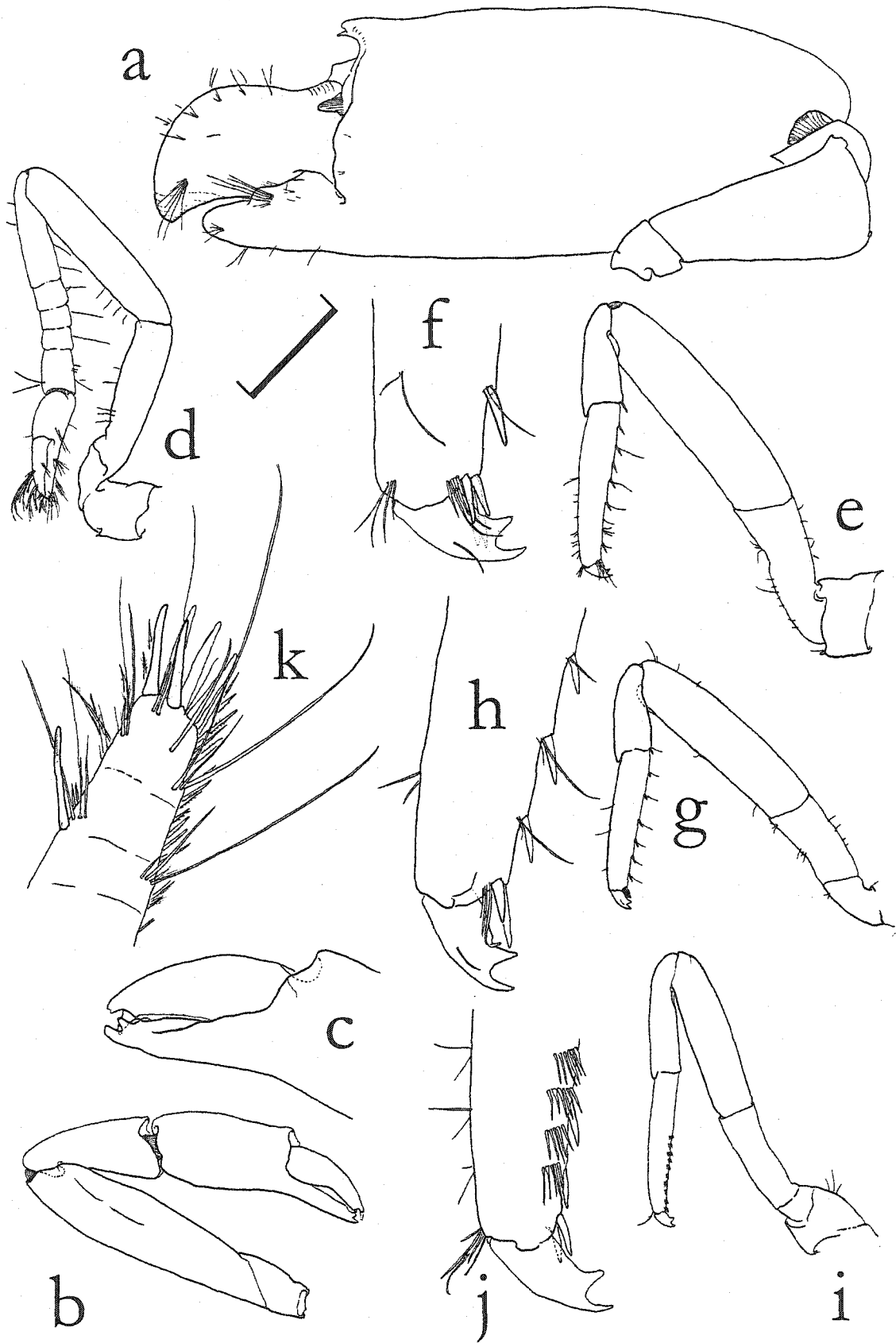
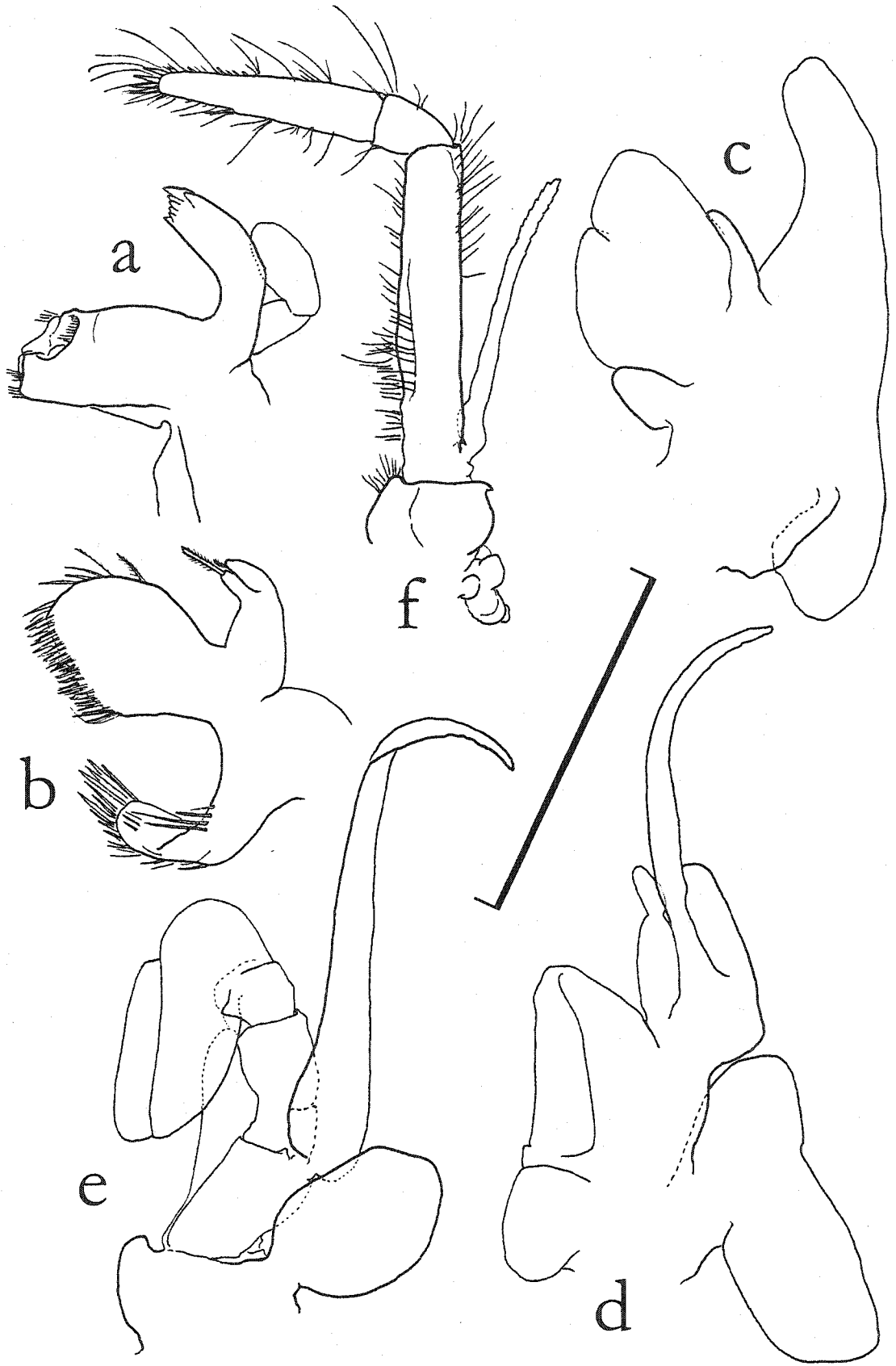


Fig. 3-4. *Synalpheus* sp. 7, new species. Mouthparts. Paratype male 4.7 mm (VIMS 93P0903): a, left mandible; b, left first maxilla; c, left second maxilla; d, left first maxilliped; e, left second maxilliped; f, right third maxilliped. Scale bar = 1 mm for a, b, c, d, e, and 2 mm for f.



## CHAPTER FOUR

### VALUE OF MORPHOLOGICAL CHARACTERS IN RECONSTRUCTING THE PHYLOGENY OF SPECIES OF *SYNALPHEUS* BATE, 1888 FROM THE WESTERN ATLANTIC (CRUSTACEA: DECAPODA: ALPHEIDAE)

**Abstract-** Because of their conservative morphology, most species of the alpheid shrimp genus *Synalpheus* Bate, 1888 have been described on the basis of a small number of characters. The majority of species in the western Atlantic belong in the Gambarelloides group, which was proposed almost a century ago by Coutière, but still lacks any formal recognition. In this study I examine the utility of a suite of morphological characters in reconstructing the evolutionary history of the Gambarelloides group of species of *Synalpheus* in the western Atlantic. By mapping 54 parsimony-informative characters of 29 species onto a tree derived from Bayesian analysis of molecular data (16S and COI), it became evident that most of the morphological characters bear a weak phylogenetic signal with frequent homoplasies. Comparisons of the information content and of the amount of evolution of groups of characters indicated no significant differences according to body region. The Gambarelloides group has the strongest bootstrap support for any of the major clades in the current phylogenetic tree. Yet, only two morphological characters are unequivocally diagnostic of the Gambarelloides group, a brush of setae on

the dorsal surface of the dactyl of the minor first pereopod, and a lamella on the coxa of the third pereopod. The setal brush was recognized as the most important character in the original designation of the groups of species of *Synalpheus* in 1908, but the coxal lamella had not been previously recorded. Similarly, two additional characters also might prove to be diagnostic for the gambarelloides group, the comparative length of the basicerite, also recognized in the original designation of the groups, and another novel structure: a tooth under the first segment of the antennular peduncle. The space between marginal spines on the distal margin of the telson, and the number of fixed teeth on the outer margin of the uropodal exopod, proved useful in diagnosing species complexes within the Gambarelloides group. The multiplicity of fixed teeth on the outer margin of the uropodal exopod is a remarkable apomorphy within the genus *Synalpheus*, rare in caridean shrimps outside this genus and indeed outside the Gambarelloides group, but common among the Gambarelloides species. A basal protuberance on the outer face of the pollex of the major chela, and the spine on the dorsolateral corner of the basicerite, both exemplify parallel evolution and are taxonomically useful. The orbitorostral process was present in only two Gambarelloides species. The blade on the scaphocerite is present and well-developed in each of the non-Gambarelloides species and reduced or completely absent in all but three of the Gambarelloides species. The weak support for the basal branches in the Gambarelloides clade prevents the tracing with certainty of the evolution of most of the morphological characters. Nevertheless, the morphological data are

phylogenetically informative enough to conclude that the Gambarelloides group of species was appropriately created on a morphological basis, and should be recognized as a subgenus of *Synalpheus* now that rigorous phylogenetic evidence is available. Moreover, despite the generally low information content of the morphological characters, they generally corroborate and add support to the relationships among *Synalpheus* species reconstructed from molecular data.

## INTRODUCTION

Phylogeny is “the appropriate theoretical background for taxonomy” (Simpson 1961). By reconstructing phylogenetic relationships the taxonomist can account for the historical speciation process, and thus the degree to which species are evolutionarily related to each other. This pattern of common ancestry provides a natural and scientifically objective basis for practical classification (Mayr 1999).

The objective of this chapter is to consider the phylogenetic utility of external morphology in reconstructing the evolutionary history of the species of *Synalpheus* snapping shrimps in the western Atlantic. Considering that phylogenetic studies deal with natural entities, a first problem to consider is the sampling, i. e. which of the known taxa are to be included? When exploring the evolutionary history of a genus, the investigator should, ideally, include every known species in a worldwide scale. In the particular case of *Synalpheus*, with more than 130 known species (Chace 1988, and Ríos, pers. obs.), the present study might appear somewhat incomplete. However, since most of the species from the western Atlantic belong in a natural grouping within the genus, known as the Gambarelloides group (Coutière 1909), I have focused on that hypothetically monophyletic group, which is well sampled and which I have studied in



detail. Historically, classifications based on morphology have proven difficult and unstable in *Synalpheus* (Coutière 1909, Banner and Banner 1975, Christoffersen 1979, Dardeau 1984). Now that molecular data have become available for most of the species in the Gambarelloides group (Duffy, Morrison and Ríos 2000, Morrison, Ríos and Duffy, in press), it is possible to objectively assess the value of the morphological characters in classifying this group. Thus, this contribution appraises the usefulness of the morphological characters most commonly used in taxonomy of *Synalpheus* for reconstructing phylogenetic relationships.

The Gambarelloides group of species within the genus *Synalpheus* was originally named “Laevimanus group” by Coutière (1908). It is one of the six groups into which he divided the genus *Synalpheus*, according to similarities among the species and a certain convergence towards the reptant decapods (lobster and crayfish). He considered that his Laevimanus group was a natural extension of his Biunguiculatus group, but with the following extreme characters: antennal scale reduced to a spine as strong as that on the basicerite, and most importantly, a grooming instrument in the form of a brush of setae on the minor first chela. In his monograph of the species from the Americas, Coutière (1909) also included the strong, even “exaggerated”, sexual dimorphism as one of the distinguishing features of this group, and a tendency toward the elongation of the carpus of the minor first chela. In a nomenclatorial twist, so frequent in this genus, Holthuis and Gottlieb (1958) included *S. laevimanus* (Heller, 1862) in the synonymy of *S. gambarelloides* (Nardo, 1847), the common sponge-dwelling shrimp from the Mediterranean Sea, consequently the name of the group was changed to “Gambarelloides”. Besides the subjective phylogenetic hypotheses conceived by Coutière (1899, 1908, 1909), based on his comprehensive knowledge of the morphology, biology and biogeography of the whole family Alpheidae, the only other publications dealing with the phylogenetic relations within a single

genus are several on selected groups of species of *Alpheus*, examined with molecular data. Knowlton *et al.* (1993) and Knowlton and Weigt (1998) analyzed the timing of isolation of morphologically defined sister species separated by the Isthmus of Panama. Williams *et al.* (2001) examined the validity of the seven groups of species that Couzière (1899, 1905) created in the genus *Alpheus*, and found that three of the groups were not monophyletic; in fact from a set of 53 putative species they identified only three major clades, of which one matched one of the groups established by Couzière. Matthews *et al.* (2002) investigated the phylogenetic and ecological relationships between *Alpheus armillatus* and the morphologically similar *A. angulosus*; they concluded that these shrimp constitute a pair of sibling species that share most of their geographical distribution, have similar ecological preferences, but maintain incompatible behavioral repertoires.

Noteworthy after years of studying the systematics of the family Alpheidae, Banner and Banner (1975) could only partially invalidate the groups of species proposed by Couzière. The present study is a continuation of our efforts (Duffy, Morrison, and Ríos 2000; Morrison, Ríos, and Duffy, in press) to understand the evolution of *Synalpheus*, and to reconstruct the relationships among its species using a more quantitative approach, namely cladistic analysis (Hennig 1966) and other modern quantitative methods (Huelsenbeck and Ronquist 2000).

## METHODS

Most specimens used in this study originated from sponges collected in the vicinity of Carrie Bow Cay, Belize, (16°48' N, 88°5' W) between 1988 and 2003. Ancillary material included specimens from the San Blas Islands, Panama, (Caribbean, 9° 34' N, 78°58' W), and from the Florida Keys, USA, (24°48'N, 80°46' W). Sponges and coral rubble were gathered

mostly by SCUBA diving, and live shrimps were hand-picked from their host, and preserved soon after collection in cold 95% ethanol or 10% formalin. The shrimps were stained with methylene blue and examined under dissecting and compound microscopes. Several individuals of each taxon were examined to assess the degree of variation within species.

Using DELTA (Dallwitz *et al.* 2000), I created a database to score 69 morphological characters by direct examination of specimens from more than 40 species of *Synalpheus* and *Alpheus cylindricus* as an outgroup taxon. For the purposes of this chapter, I am including only the species for which two gene segments, namely the mitochondrial cytochrome oxidase I (COI) and 16 S ribosomal RNA (16S) genes, also have been sequenced (Morrison, Ríos and Duffy in press). Phylogenetic hypotheses were obtained with PAUP 4.0b10 (Swofford 2002) using parsimony as the optimality criterion, for heuristic searches on best trees only, starting trees obtained via stepwise addition, swapping on 1000 random addition replicates, enforcing tree bisection-reconnections as the swapping algorithm. Bootstrap support was calculated after 1000 replicates with 41 random additions each.

To investigate the evolution of morphological characters, the morphological character data matrix was mapped with MacClade 4.03 (Maddison and Maddison 2001) onto a tree obtained by Bayesian analysis (Huelsenbeck and Ronquist 2000) of the molecular data, including both 16S and COI sequences (Morrison, Ríos and Duffy in press); this tree was trimmed to include only the 30 species for which morphological data were available. Furthermore, to investigate correlated patterns of evolution among the morphological characters, five groups of characters were designated according to different body regions: carapace (characters 1-10), head (characters 11-24), pereopods (characters 25-44), abdomen (characters 45-49), and tail fan (telson + uropods; characters 50-54). The average rescaled consistency index, or RCI (Farris

1989), and average number of changes along the tree, were calculated for each class of characters, and compared, as measures of phylogenetic utility and relative amount of evolution, respectively. RCI values for each character were calculated as:

$$\text{RCI} = (\text{character CI}) \times (\text{character RI});$$

$$\text{where CI} = m/s \text{ and RI} = (M-s)/(M-m),$$

$m$  is the minimum possible number of steps,  $M$  is the maximum possible number and  $s$  is the number of reconstructed steps for each given character. RCI ranges from 0 to 1.

## RESULTS

Of the 69 morphological characters that I have compiled in reviewing the *Synalpheus* of the world, a subset of 54 characters are phylogenetically informative (Table 4-1) when dealing with the complete species list from the western Atlantic. However, four of those are autapomorphic and thus uninformative in the array of species included in the analysis of the present chapter (Tables 4-1 and 4-2).

Unweighted parsimony analysis of the morphological data set produced 281 trees (264 steps) and a poorly resolved consensus tree (Fig. 4-1). This consensus tree is almost identical to the trimmed morphological character tree based on the extended set of taxa (Fig. 1C from Morrison, Ríos and Duffy in press), with only two minor changes in the latter analysis: species 6 (=“pandionis small” of Morrison, Ríos and Duffy in press) was the sister taxon of species 7 (=“pandionis red”) with a support of 59%, and *S. rathbunae* was the sister species of *S. regalis* (54%). The only significant bootstrap support (>50%) in the present analysis based on morphology is for the clades defining the Gambarelloides group of species (69%), and the Neomeris group of species (92%), the latter represented only by *S. dominicensis* and *S. fritzmulleri*.

An incongruence length difference test (Farris et al. 1995) comparing the consensus tree from the Bayesian analysis of the combined (COI and 16S) molecular data (Fig. 4-1) with the morphology tree revealed no significant incongruence (Morrison, Ríos and Duffy in press). Indeed, when both molecular and morphological characters were combined in a single parsimony analysis, the resultant topology (Fig. 4-2) was consistent with each of the single data sets (COI, 16S, morphology), but had increased support for several clades relative to any single data set. The main difference between the Bayesian tree and the combined data tree is the rearrangement of several weakly supported branches inside the clade that includes *S. longicarpus*.

Comparing the number of steps for each morphological character in each of these two trees (Fig. 4-3), the combined tree is shorter for 12 characters, while the molecular tree is shorter only for 4 characters, indicating that the phylogenetic signal of the morphology adds more parsimony to the analysis. The phylogenetic signal of characters, as measured by the rescaled consistency index (RCI), did not differ significantly on average among the five groups of morphological characters (Fig. 4-4,  $P=0.71$ , ANOVA). Nor did the amount of evolution, expressed in number of changes, differ among the 5 groups of characters (Fig. 4-5,  $P=0.47$ , ANOVA). A further partition of the groups, *i. e.* isolating the characters from the first periopods, did not provide any additional information although the number of characters in these partitioned groups are too small to test this rigorously.

The phylogenetic signal (RCI) for each character is negatively correlated ( $P=0.04$ , linear regression) with the amount of evolution (number of changes) in each character (Fig. 4-6) indicating that rapidly evolving characters are of little phylogenetic utility in this group. The frequency distribution of maximum number of changes and of RCI values among morphological characters (Fig. 4-7) shows that most of these latter provide little phylogenetically

useful information, with 15 of them having RCI= 0 (no more informative than a randomly changing character) and only two of them amounting to 1 (best possible fit on the tree).

The patterns of evolution of particular characters (Figs. 4-8 through 4-12) provided insight into the phylogenetic utility of characters historically used in *Synalpheus* taxonomy, as well as some newly described ones. Only two consistent diagnostic morphological synapomorphies define the Gambarelloides clade (Fig. 4-8). First, the brush of setae on the dactyl of the minor first pereiopod (character 34) is one of the characters that Coutière (1908, 1909) originally adduced when creating his group of species. Second, I have discovered that the coxal lamella on the third pereiopod (character 44) is also consistent among species in the Gambarelloides group (Fig. 4-8). My analysis also has identified two additional characters that characterize the Gambarelloides group, although they are somewhat less consistent than the two just mentioned (Fig. 4-9). These are the length of the ventrolateral spine of the basicerite in relation to the stylocerite (character 20) and the ventromesial tooth on the first segment of the antennular peduncle (character 17). *Synalpheus longicarpus* has undergone a regression of character 20, whereas *S. mcclendoni* and *S. sanctithomae* have independently regained the tooth in character 17.

Two features widely used in taxonomy of *Synalpheus*, the orbitorostral process (character 8) and the blade on the scaphocerite (character 21) have contrasting evolutionary histories that appear to contain little or no phylogenetic signal (Fig. 4-10). The orbitorostral process has evidently developed thrice independently, whereas no pattern is clear for the scaphocerite blade, which has changed numerous times throughout the tree.

My analysis identified a few characters that proved useful in diagnosing species complexes within the Gambarelloides group (Fig. 4-11). These include the space between the distal spines of the telson (character 50), and the number of fixed teeth on the outer margin of

the uropodal exopod (character 54). Each of these characters is fairly consistent within clades of closely related species within the Gambarelloides group.

Finally, I depict the history of two characters that appear to exemplify parallel evolution within *Synalpheus*, that is, each of them is gained separately in different lineages (Fig.4-12). These are a basal protuberance on the outer face of the pollex of the major chela (character 27) and the spine on the dorsolateral corner of the basicerite (character 19). Despite an otherwise poorly informative phylogenetic signal, these characters are taxonomically useful and help to distinguish closely related species.

#### DISCUSSION

The availability of a revised phylogeny of the *Synalpheus* from the western Atlantic (Morrison, Ríos and Duffy in press) provides a valuable framework for the study of the evolution of this genus. In order to avoid circularity (*vide* de Queiroz 2000), I have chosen to conduct the analysis of the morphological characters on a molecular-data reconstruction (Fig.4-1). Although this potentially sacrifices the best estimation of the phylogeny (Fig. 4-3), namely the one that contains all available data, including the morphological information (Fig. 4-2), in fact there is no significant conflict between the morphological and molecular trees (Fig. 4-1). Thus, the Bayesian reconstruction of the molecular data set is probably the best choice as an independent tree for analyzing morphological evolution. This is demonstrated by the support of most of the same clades in the Bayesian (Fig. 4-1) and the combined data (Fig. 4-2) tree. Also, as Morrison, Ríos and Duffy (in press) indicate, similarly to the combined tree, the Bayesian tree is the only molecular tree supporting the monophyly of the Gambarelloides group.

The present analysis suggests that phylogenetically informative morphological characters are rather scarce in the genus *Synalpheus*, and they do not seem to be concentrated in any particular region of the body (Figs. 4-4 and 4-5). Both the number of changes and the RCI per character (Figs. 4-6 and 4-7) indicate that most of the morphological characters have changed frequently during the evolution of the Gambarelloides group, rendering them relatively uninformative for phylogenetic reconstruction. The two characters with the highest RCI values are, not coincidentally, the most important in defining the Gambarelloides group of species. First, the setal brush on the dactyl of the minor chela was traditionally recognized as one of the synapomorphies of the group (Coutière 1908, 1909), despite its incomplete reversal in *S. paraneptunus*. The second character, the coxal lamella on the third leg (Fig. 4-8), had not been previously recorded. My analysis shows that two additional characters might also be diagnostic for the Gambarelloides group: the length of the ventrolateral spine of the basicerite compared to the stylocerite (RCI= 0.40), already mentioned by Coutière (1909), and the tooth under the first segment of the antennular peduncle (RCI= 0.22). With regard to the first of these characters, *S. longicarpus* is the only species within the group with a short basicerite, whereas both *S. mcclendoni* and *S. sanctithomae* are the only Gambarelloides species that have regained the mentioned tooth (Fig. 4-9). A carina under the first segment of the antennular peduncle was frequently used in the revision of the *Alpheus* from the Eastern Pacific (Kim and Abele 1988), but the tooth in *Synalpheus* has been previously overlooked. Another morphological feature herein recorded for the first time, the ventral basal processes on the first antenna (RCI= 0.22) seem to be associated to the brevicarpus group of species, but with only two recognized species in the western Atlantic (*S. minus* and *S. brevicarpus*) such a result remains to be confirmed.



Interestingly, the orbitorostral process (RCI= 0), frequently mentioned in the literature but still vaguely defined, was present in only two Gambarelloides species, and in the two species from the neomeris group (*S. fritzmulleri* and *S. dominicensis*) (Fig. 4-10). Banner and Banner (1975) did not concede any value to this character, and announced a paper dedicated to discuss it at large; but unfortunately it was never published. Detailed attention to the orbitorostral process is necessary to clarify its potential phylogenetic value, since my observations suggest that more than one thing has been given the same name. In some species there is a deep ventral keel on the rostrum, but I have retained the name "orbitorostral process" strictly for a typically bifurcated, massive projection under the base of the rostrum which continues itself on the ventro-mesial margin of each ocular hood.

The blade on the scaphocerite, a well defined structure on the antennal peduncle, is conspicuously present in each of the non-Gambarelloides species examined (Fig. 4-10). It is reduced or completely absent in all of the Gambarelloides species, except *S. mcclendoni*, *S. sanctithomae* and *S. pandionis*. Coutière (1908, 1909) mentioned this tendency toward loss of the blade as one of the characteristics of the Gambarelloides group. Subsequent authors (*e. g.*, Christoffersen 1979 and Dardeau 1984) have considered that this character is highly variable at the intraspecific level; however, the material examined for this study indicates that such intraspecific variation is not very common and is restricted to the size of the blade, without affecting its shape. My taxonomic study (Chapter 2) shows instead that much of the variation in this character previously considered to be within species actually occurs among closely related (cryptic) species, which are preliminarily described in that chapter. In *S. androsi*, I have recorded that the megalopa larva has a fully developed blade, which is completely lost during the ontogenetic development. The blade on the scaphocerite is a fine example of the phylogenetic

pattern of most morphological characters of *Synalpheus* with high frequency of homoplasies. In this case, following an apparent total loss of the blade in the basal clade of the Gambarelloides, the most parsimonious tree suggests that it reappeared at least in six different occasions (Fig. 4-10). It must be emphasized, however, that even the combined analysis of all molecular and morphological data produced a tree with weak support for the relationships among the basal branches in the Gambarelloides clade. Thus, it is difficult to trace with certainty the evolution of such a frequently changing character.

Coutière (1899) noticed in some species of *Synalpheus* a reduction in width of the posterior margin of the telson in contrast to a generally wide state in *Alpheus*, whose species, he considered, converge to a more lobster-like design. Tracing the history of this character (Fig. 4-11), it becomes apparent that in most of the Gambarelloides species of *Synalpheus* the hiatus between the distal marginal spines of the telson is reduced, and that such feature is consistent within complexes of closely related species. Interestingly, this character is an exception to the general tendency that Coutière (1909) recognized in the Gambarelloides species to resemble reptant forms.

The multiplicity of fixed teeth on the outer margin of the uropodal exopod is a remarkable apomorphy within the genus *Synalpheus*. Despite its absence in most of the species in the clade that includes *S. boussfieldi*, and in three other species (Fig. 4-11), the presence of multiple uropod teeth seems to be restricted to the Gambarelloides group and is found nowhere else within the family Alpheidae. Except in cases of polymorphism, in which the same species may have one or two teeth, this character is easy to score and has consequently been widely used as a diagnostic character at the species level in *Synalpheus*. The material examined for this study suggests that not only the number of teeth is important, but also the arrangement they keep in

relation to the mobile and the fixed spines on the uropodal exopod. For example, in *S. goodei* the submesial fixed tooth is wider than in *S. williamsi* and also, the mobile spine is much shorter.

The evolutionary history of the protuberance on the pollex of the major chela, which I call the “Williamsian protuberance” after *S. williamsi*, in which this character is well developed, and the dorsal spine on the basicerite (Fig. 4-12), illustrate two cases of parallelism as defined by Simpson (1961): each of them appears to have arisen separately in two or more lineages of common ancestry. This kind of morphological character provides a weak phylogenetic signal, but can be taxonomically important. These are discrete traits easy to record, and aid in distinguishing species otherwise closely related.

This phylogenetic analysis of the relations among the western Atlantic species of *Synalpheus* substantiates some of the observations by Coutière (1908, 1909) and Banner and Banner (1975). Most notably, I support the conclusion that the Gambarelloides group of species is a monophyletic clade, *i. e.*, a natural assemblage. This conclusion further adds to the need for revision of the taxonomic status of *Synalpheus* as a genus, already foreseen by Banner and Banner (1975). If the genus is subdivided, the name *Synalpheus* would remain for the Comatularum group of species (Chace 1988), whereas the only other known name available (*Homaralpheus* Bate) would belong to the Brevicarpus group of species (see Holthuis 1993). Probably, a most conservative approach for the time being, would be to recognize a formal subgeneric status for the Gambarelloides group, as Williams *et al.* (2001) have suggested for the three clades of *Alpheus* they recognized.

Unlike the case of the Asellota isopods (Wägele *et al.* 2003), another traditionally accepted crustacean clade, in the Gambarelloides group the molecular analysis generally

supports the taxonomy based on the detailed morphological accounts of M. Henri Coutière, a naturalist from the early 20<sup>th</sup> century. More generally, previous authors have often found that even when morphological and molecular characters appear to conflict, closer analysis shows that they often provide positive support for the same tree (*e. g.*, Baker *et al.* 1998; Cannatella *et al.* 1998). Even the most outspoken advocates of molecular-data based phylogenetic studies, still recognize the relevance of morphological studies in phylogeny reconstruction (see Scotland *et al.*, 2003).

The analysis presented here indicates that few of the morphological characters bear an informative phylogenetic signal in *Synalpheus*, and most of them are homoplasies. The taxonomic consequences of this perspective are reflected in the history of some of the species names in the genus, like *S. longicarpus* and *S. pandionis* (see remarks in Chapter 1), since different authors have emphasized different characters when classifying *Synalpheus*.

The low phylogenetic information content and frequent homoplasy of morphology in *Synalpheus* raise the question of what evolutionary processes might be responsible. The difficult taxonomy and the distribution of morphological characters of the western Atlantic *Synalpheus* might result from a rapid radiation of this group during closure of the Panamanian seaway, a conclusion supported by molecular evidence (Morrison, Ríos and Duffy, in press). Such a rapid radiation could be responsible for the absence of hierarchically nested sets of morphological characters necessary to reconstruct an accurate phylogeny. Knowledge of functional morphology could aid in interpreting patterns of evolution in morphological characters. Unfortunately, the limited information prevents us from further interpreting the histories of most of the morphological characters in this fascinating group of shrimp. Further study of

functional morphology promises to yield important insights into this enigmatic and fascinating taxon.

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Table 4-1. List of parsimony-informative morphological characters used in phylogenetic analysis of western Atlantic *Synalpheus*, with description of the states. Numbers correspond to those in Table 4-2.

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1.	Carapace texture: 1, glabrous; 2, sparsely setose.
2.	Pterygostomial corner: 1, acute; 2, obtuse.
3.	Posterior margin of carapace with cardiac notch: 1, distinct; 2, diminished.
4.	Rostrum, compared to orbital teeth: 1, clearly narrower; 2, about as wide; 3, wider.
5.	Rostrum, compared to orbital teeth: 1, noticeably shorter; 2, about as long; 3, clearly longer.
6.	Rostrum: 1, distally upturned; 2, not upturned.
7.	Rostrum margins in dorsal view: 1, straight; 2, concave; 3, convex.
8.	Orbitorostral process: 1, absent; 2, present.
9.	Ocular hoods, shape in dorsal view: 1, sharply acute; 2, acute; 3, obtuse; 4, squarely rounded; 5, bluntly triangular.
10.	Adrostral sinus: 1, deep; 2, shallow.
11.	Ocular processes: 1, absent; 2, present, but not elongated; 3, produced.
12.	Ocellary beak: 1, rod-like; 2, not rod-like.
13.	Stylocerite: 1, slender; 2, stocky.
14.	Stylocerite, mesial margin: 1, slightly concave; 2, straight; 3, convex.
15.	Stylocerite: 1, acute; 2, blunt.
16.	Stylocerite, length compared to distal margin of first segment of antenna 1: 1, clearly exceeding; 2, about the same; 3, distinctly shorter.
17.	Ventromesial tooth on first segment of antenular peduncle: 1, present; 2, absent.

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(Continued)

Table 4-1. (Continued) List of parsimony-informative morphological characters used in phylogenetic analysis of western Atlantic *Synalpheus*, with description of the states. Numbers correspond to those in Table 4-2.

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18. Ventral basal processes on antenna 1: 1, none; 2, one; 3, two.
  19. Spine on dorsolateral corner of basicerite: 1, absent; 2, present.
  20. Ventrolateral spine of basicerite compared to tip of stylocerite: 1, clearly overreaching; 2, not overreaching.
  21. Scaphocerite blade: 1, present; 2, reduced; 3, absent.
  22. Lateral margin of scaphocerite: 1, straight; 2, slightly concave.
  23. Scaphocerite spine compared to antennular peduncle: 1, not overreaching; 2, clearly overreaching.
  24. Mesial projection at base of scaphocerite: 1, absent; 2, present.
  25. Fingers of major first pereiopod compared to half length of palm: 1, clearly not longer; 2, clearly longer.
  26. Pollex of major first pereiopod compared to dactyl: 1, about as long; 2, reduced; 3, longer.
  27. Protuberance on outer face of pollex of major chela: 1, absent; 2, present.
  28. Kind of projection on superior distal margin of palm of major chela: 1, prominent blunt tubercle; 2, prominent tubercle with acute spine; 3, tapering acute spine.
  29. Extensor margin of merus of major first pereiopod: 1, straight or slightly convex; 2, strongly convex.
  30. Extensor margin of merus of major first pereiopod: 1, with distinct distal spine; 2, with flat distal angular projection; 3, ending in acute angle; 4, ending in right angle; 5, ending in obtuse angle.
  31. Palm of minor first chela: 1, clearly less than two times longer than high; 2, about two times longer than high; 3, more than twice as longer as high.
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(Continued)

Table 4-1. (Continued) List of parsimony-informative morphological characters used in phylogenetic analysis of western Atlantic *Synalpheus*, with description of the states. Numbers correspond to those in Table 4-2.

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32. Number of teeth on dactyl of minor first chela: 1, one; 2, one with subdistal accessory bump; 3, two or three, subequal in length.
33. Arrangement of dactyl teeth on minor first chela in relation to dactyl axis: 1, perpendicular; 2, parallel.
34. Transverse dorsal setal combs on dactyl of minor first chela: 1, absent; 2, very conspicuous; 3, much reduced.
35. Number of teeth on pollex of minor first chela: 1, one; 2, one with subdistal accessory bump; 3, two subequal in length.
36. Extensor margin of merus of minor first pereiopod: 1, straight; 2, convex.
37. Extensor margin of merus of minor first pereiopod: 1, with distinct distal spine; 2, with flat distal angular projection; 3, ending in acute angle; 4, ending in right angle; 5, ending in obtuse angle.
38. Segments on carpus of second pereiopod: 1, five; 2, four.
39. Second pereiopod, carpus/merus length relation: 1, >1; 2, =1.
40. Third pereiopod: 1, slender; 2, stout.
41. Relative size of unguis on dactyl of third pereiopod: 1, subequal; 2, clearly unequal.
42. Unguis, widest at base: 1, extensor; 2, flexor.
43. Movable spines on flexor margin of merus of third pereiopod: 1, absent; 2, present.
44. Mesial lamella on coxa of third pereiopod: 1, absent; 2, present.
45. First abdominal pleura of male with posterior corner: 1, weakly produced, or rounded; 2, strongly produced posteriorly; 3, acutely produced ventrally; 4, distinctly produced ventrally and anteriorly, hook-like.
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(Continued)

Table 4-1. (Continued) List of parsimony-informative morphological characters used in phylogenetic analysis of western Atlantic *Synalpheus*, with description of the states. Numbers correspond to those in Table 4-2.

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46. Second abdominal pleura of male: 1, rounded to obtuse; 2, produced posteriorly into acute projection; 3, produced both anteriorly and posteriorly into acute projections.
  47. Terminal setae on endopod of male first pleopod: 1, five or less; 2, six or more.
  48. Second pleopod of male with marginal setae on exopod originating: 1, close to base; 2, near midpoint.
  49. Appendix interna on second to fifth male pleopods: 1, present; 2, absent.
  50. The space between distal spines of telson compared to one-third of its distal margin: 1, greater; 2, equal or less.
  51. Convex lobe on distal margin of telson: 1, present; 2, absent.
  52. Posterior corners of telson: 1, obtuse; 2, rectangular; 3, acute.
  53. Postanal setal brush: 1, absent; 2, present.
  54. Number of fixed teeth on outer margin of uropodal exopod: 1, one; 2, more than one.
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Figure 4-1. Phylogenetic hypotheses for 39 western Atlantic species of *Synalpheus*, and *Alpheus cylindricus* as an outgroup. Left: Tree based on morphological data, strict consensus of 281 most parsimonious trees (264 steps). Figures above branches are bootstrap support (N=1000 replicates with 31 random additions each). Right: Tree based on combined molecular (COI and 16S) data, redrawn from Morrison, Ríos and Duffy (in press). Consensus tree produced from 9801 sampled trees in Bayesian analysis (1 million generations). Numbers above branches are clade credibility values.

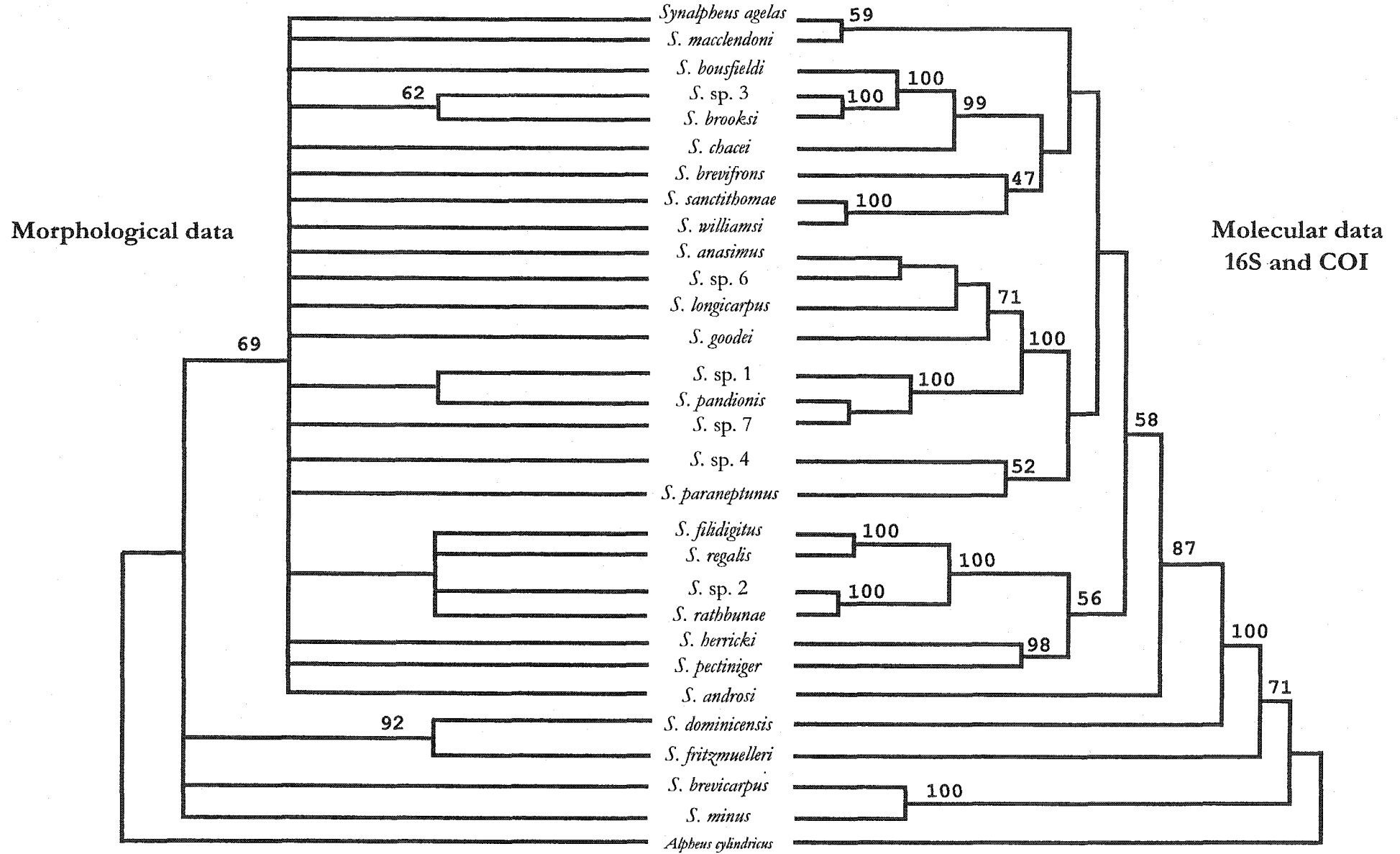
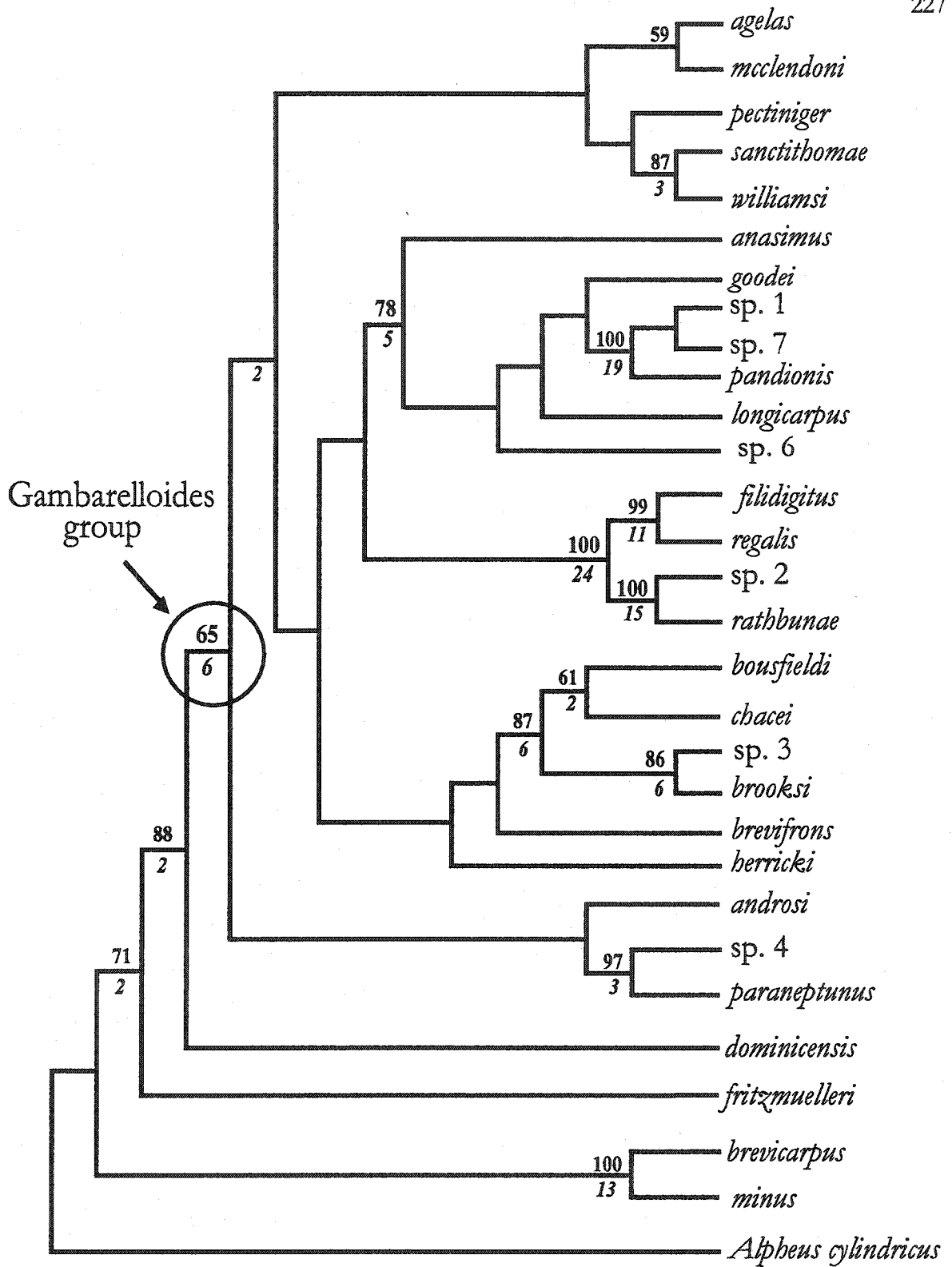


Figure 4-2. Phylogenetic hypothesis for 39 western Atlantic species of *Synalpheus*, and *Alpheus cylindricus* as an outgroup, based on combined molecular (COI and 16S) and morphological characters using weighted parsimony. Single most parsimonious tree is shown (502 informative characters, 4837 steps, Consistency index= 0.2349, Retention index= 0.4720). Numbers above branches are bootstrap values (1000 replicates, 100 random additions/replicate), and numbers below branches refer to decay indices (Bremer support) calculated using the unweighted consensus tree (redrawn from Morrison, Ríos and Duffy in press).





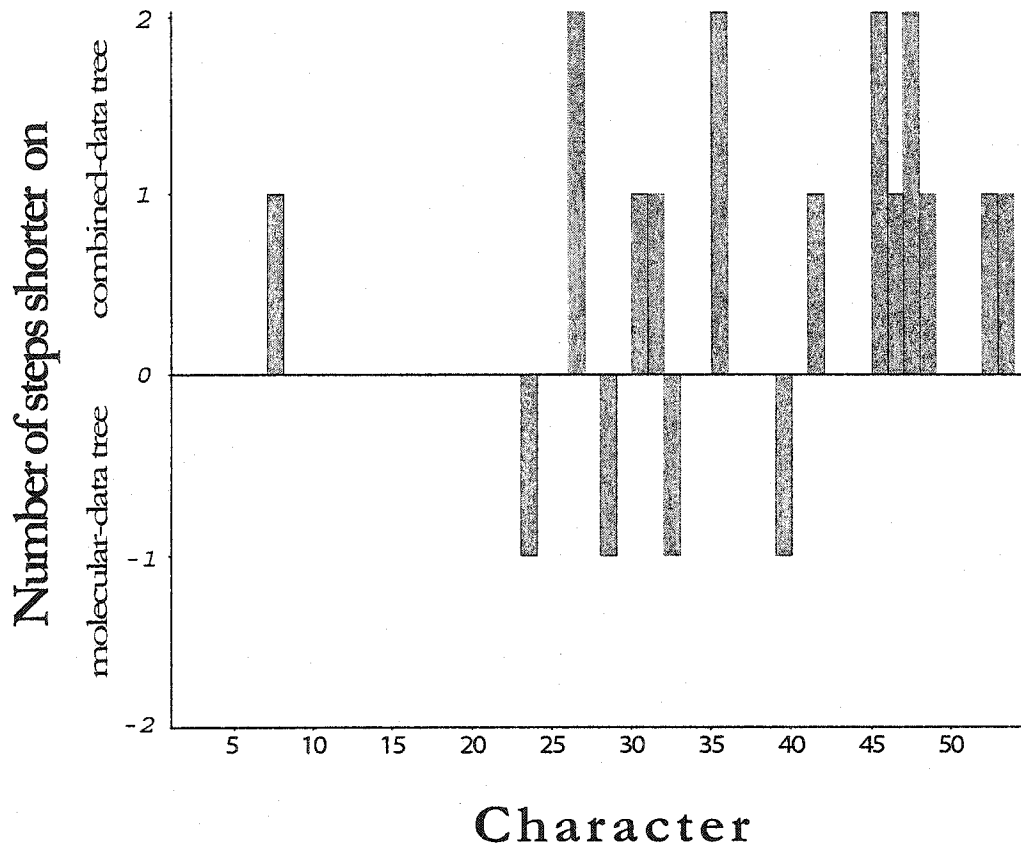


Figure 4-3. Comparison of the relative fit of each morphological character to the best tree from combined molecular and morphological data (Fig. 4-2), versus on the best tree from molecular data only (Fig. 4-1). Plotted for each character is the difference in number of steps on the molecular-data tree vs. the combined-data tree; positive values point out the cases when the combined tree is shorter, and vice versa. The contribution of the morphological data is manifest in the more frequent shorter trees in the combined data set.

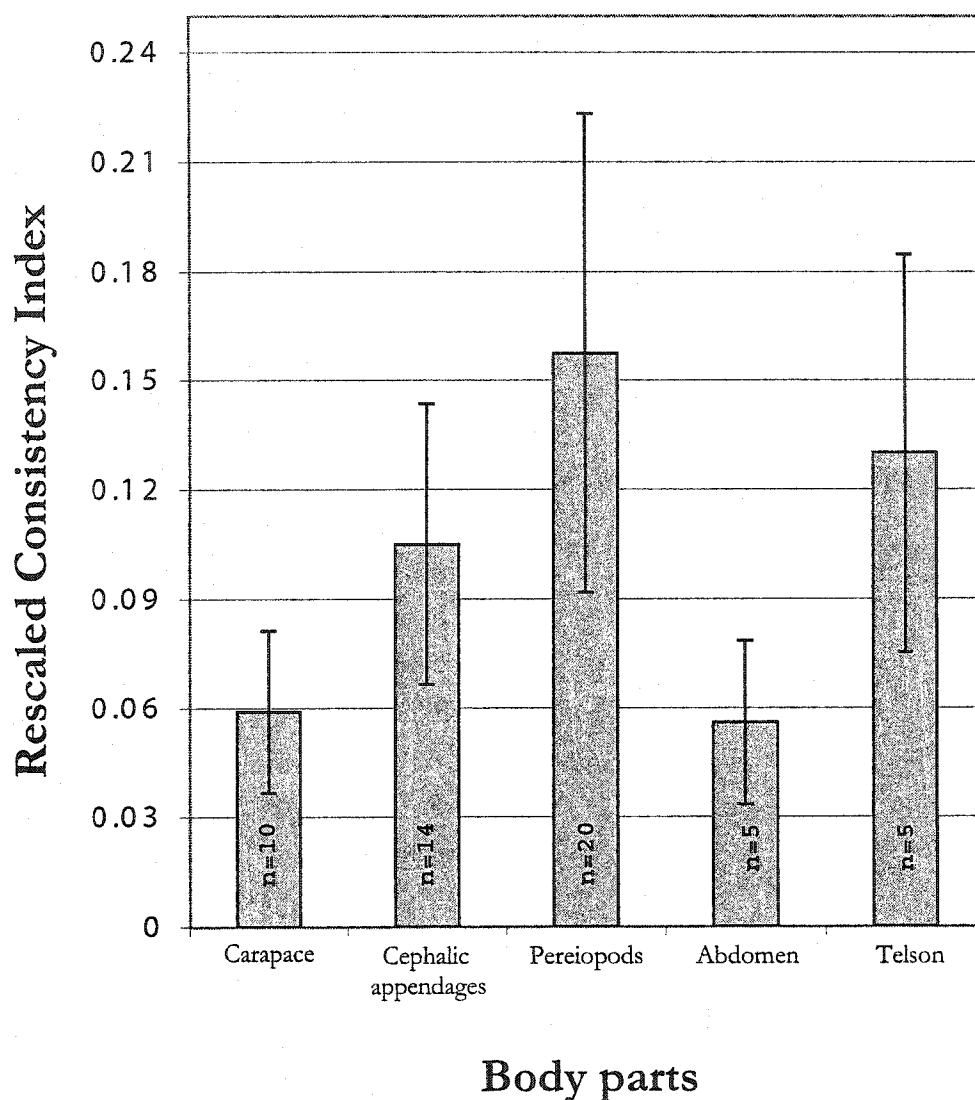


Figure 4-4. Comparison of the phylogenetic information content of five groups of morphological characters of *Synalpheus*. Data are the mean ( $\pm 1$  SE) Rescaled Consistency Index (RCI) for each group, plotted on the tree obtained from molecular data only (Fig. 4-1). The number of characters included in each group are shown at base of bar. There was no significant difference in RCI among characters from the different body regions ( $P = 0.71$ , ANOVA).

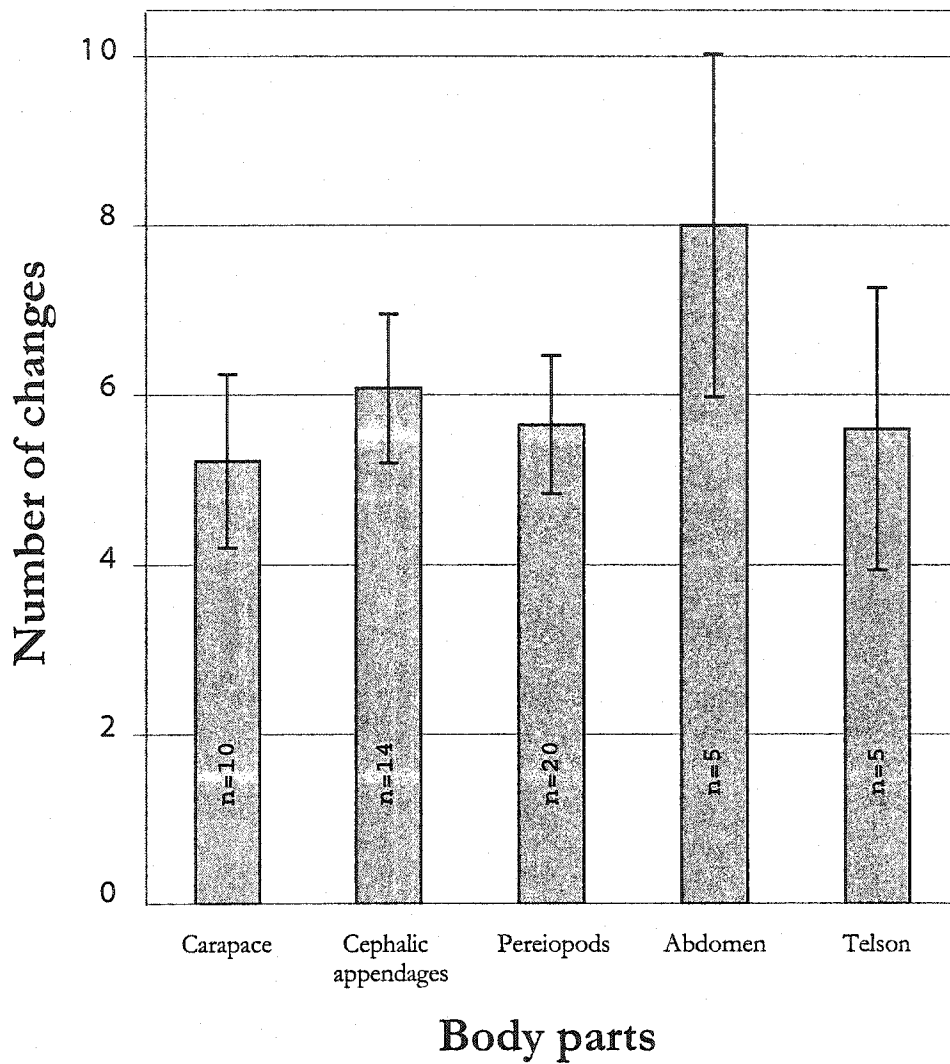


Figure 4-5. Comparison of the amount of evolution of five groups of morphological characters of *Synalpheus*. Data are the average number of changes per character for each group, plotted on the tree obtained from molecular data only (Fig. 4-1). The number of characters included in each group are shown at base of bar. There was no significant difference in number of changes among characters from the different body regions ( $P = 0.48$ , ANOVA).

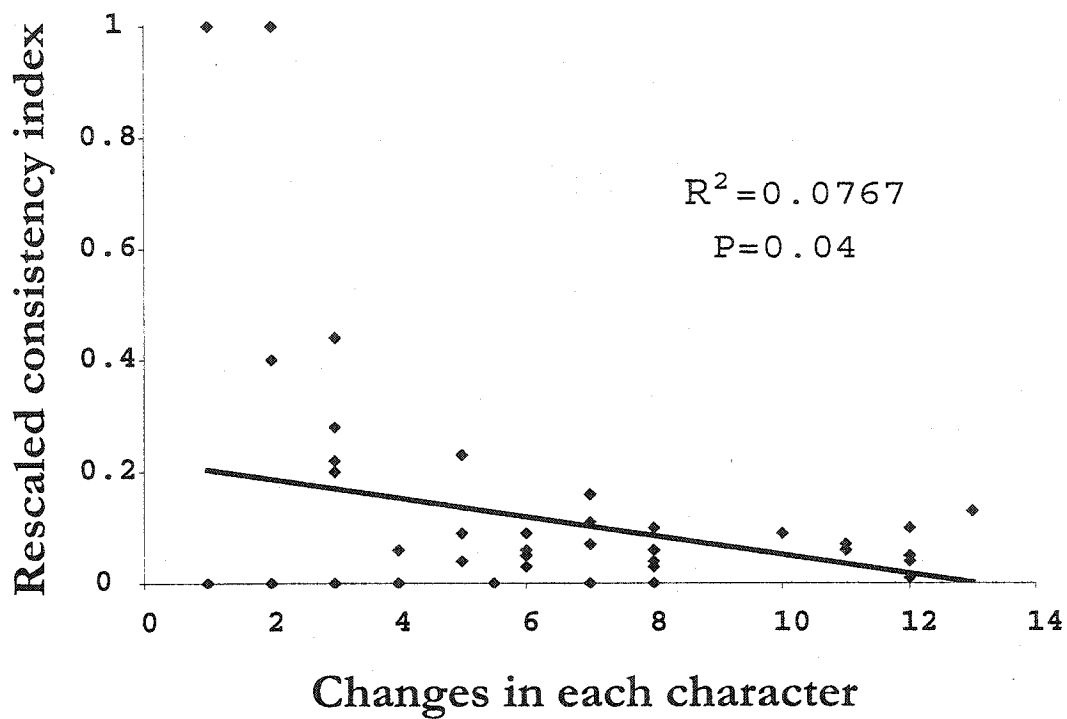


Figure 4-6. Rescaled Consistency Index as a function of the number of changes in each morphological character of *Synalpheus*. The RCI decreases significantly ( $P = 0.04$ , linear regression) with the amount of evolution (i. e., number of changes) in a character.

Figure 4-7. Variability of the morphological characters of *Synalpheus*. Top: Frequency distribution of number of changes in each character. Bottom: Frequency distribution of the Rescaled Consistency Index among characters.

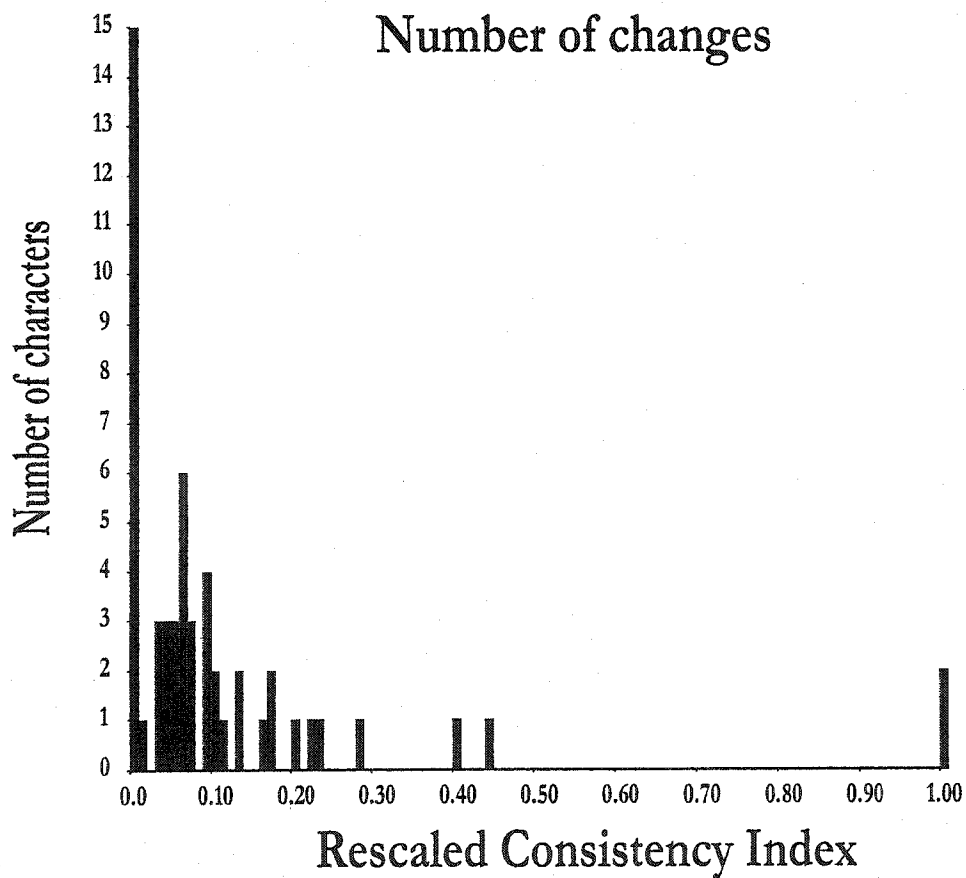
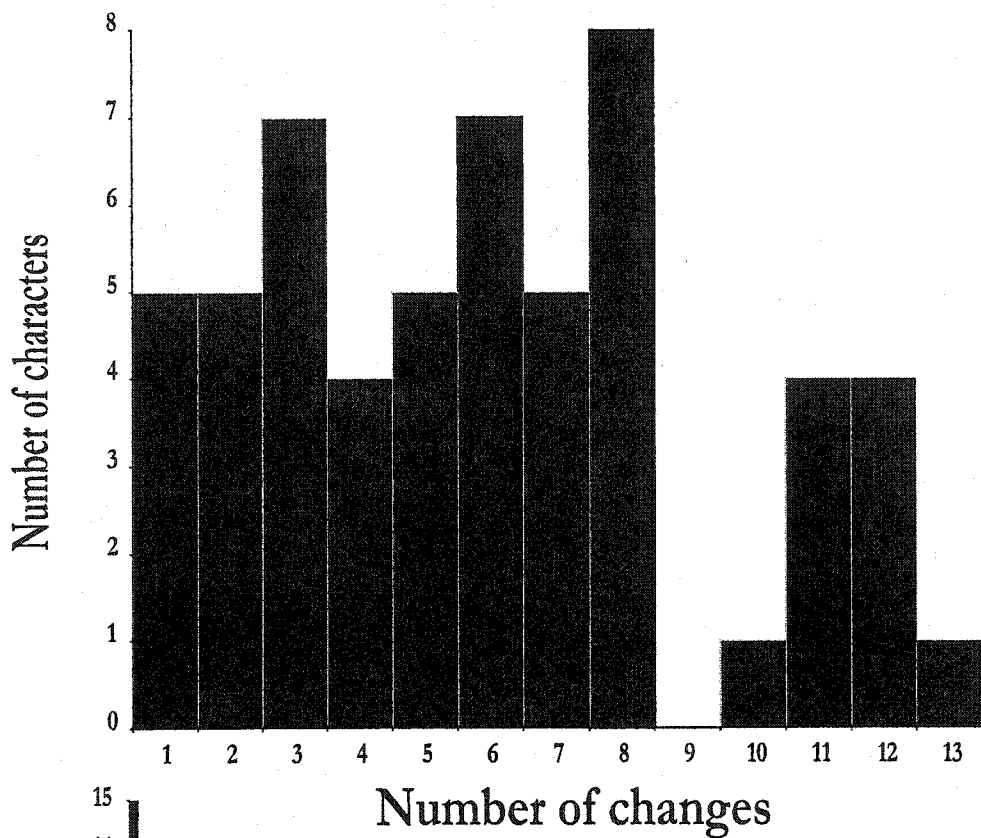


Figure 4-8. Evolutionary history of two diagnostic characters of the Gambarelloides species group: character 34 (Absence or presence of a brush of setae on the dactyl of the minor first pereiopod) and character 44 (Absence or presence of a coxal lamella on the third pereiopod). In both trees, the ancestral state in black indicates the lack of the structure and the derived state in red indicates its possession; *Synalpheus paraneptunus* has undergone a partial regression (in green) of character 34.



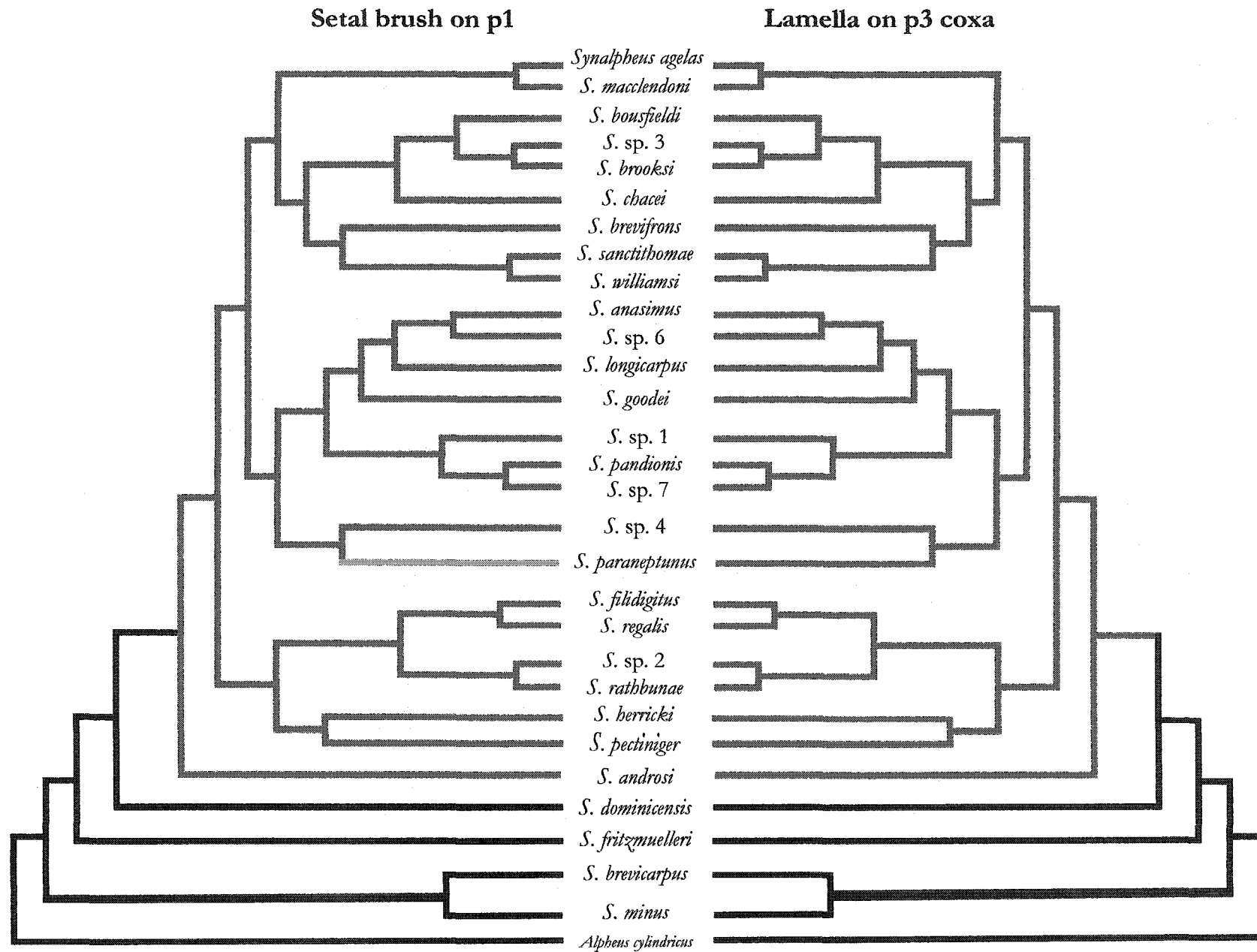


Figure 4-9. Evolutionary history of two additional characters useful in diagnosing the *Gambarelloides* species group: character 20 (Ventrolateral spine of basicerite compared to tip of stylocerite) and character 17 (Absence or presence of a ventromesial tooth on the first segment of the antennular peduncle). In the tree on the left, the ancestral state in black indicates that the stylocerite falls short of the basicerite. In the tree on the right, the ancestral state in black indicates that the tooth is present. The derived state is depicted in red in both trees.

Basicerite spine vs stylocerite

AP, tooth under first segment

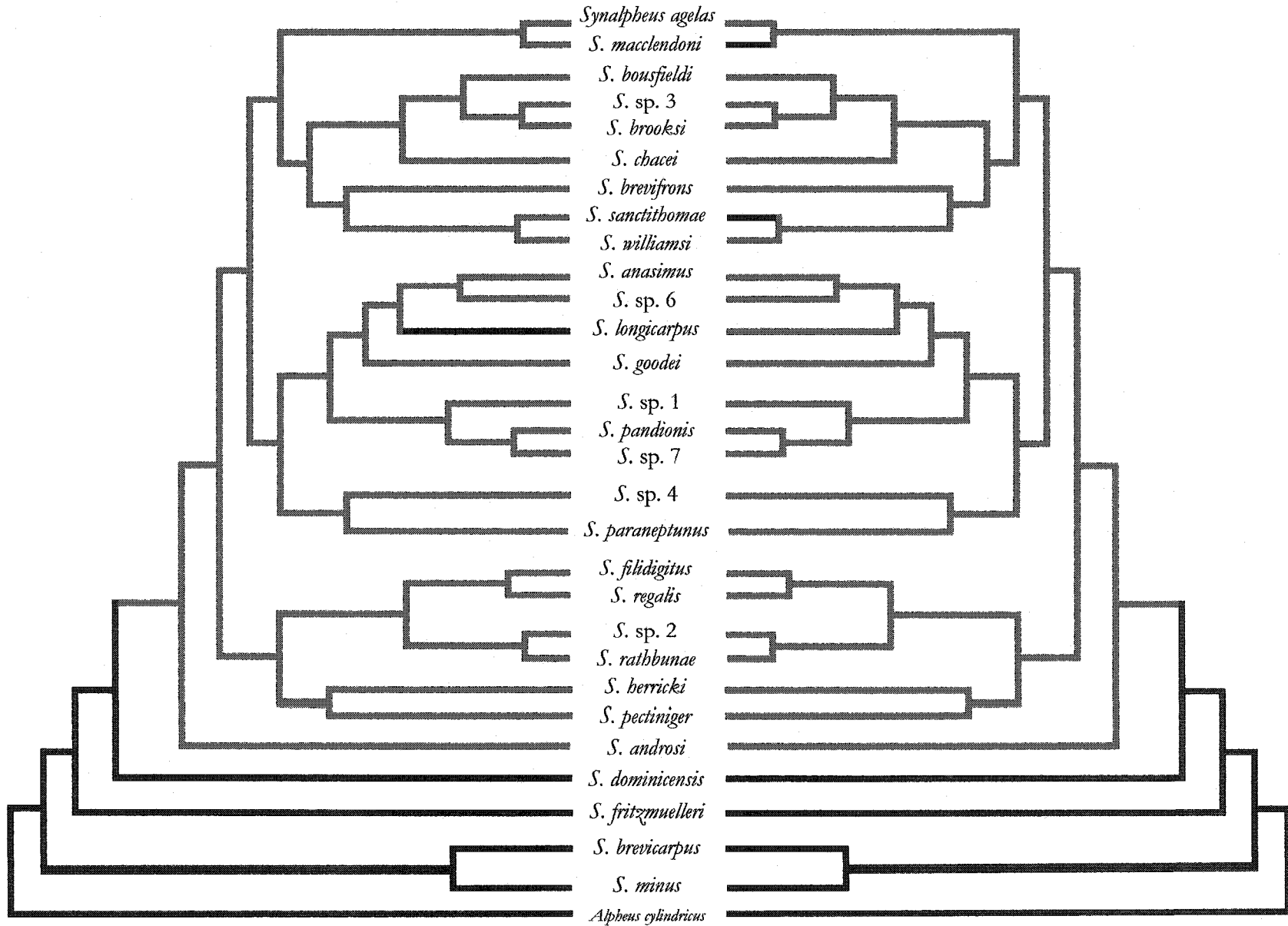


Figure 4-10. Evolutionary history of two characters traditionally used in *Synalpheus* taxonomy, character 8 (Absence or presence of orbitorostral process) and character 21 (Absence or presence of a blade on the scaphocerite). In the tree on the left, the ancestral state in black indicates that the orbitorostral process is absent, the derived state in red indicates that it is present. In the tree on the right, the ancestral state in black indicates that the scaphocerite blade is present, the derived state in red indicates its absence, and a reduced blade is indicated in green. The violet indicates ambiguous ancestral states in both trees.

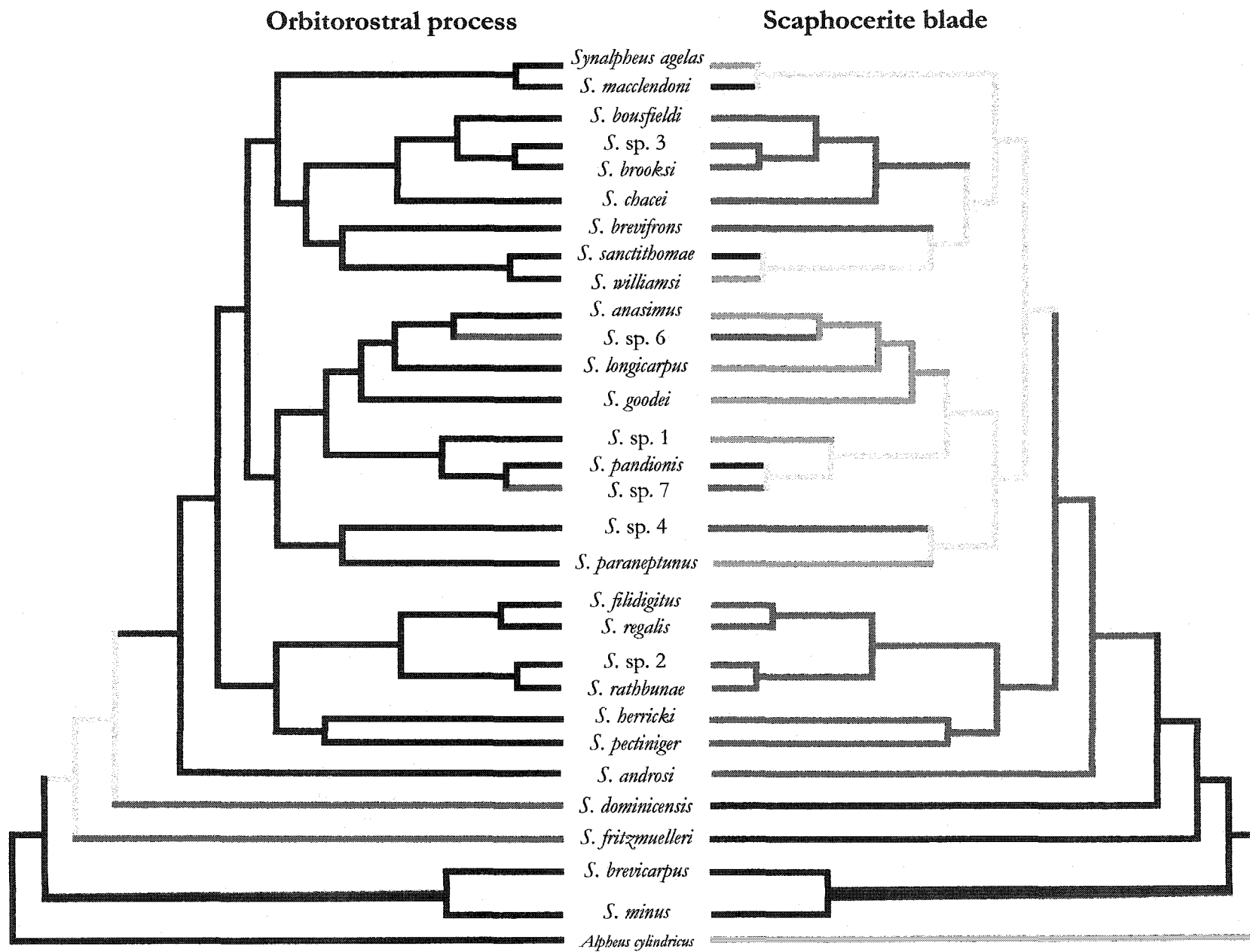


Figure 4-11. Evolutionary history of character 50 (The space between the distal spines of the telson) and of character 54 (Number of fixed teeth on the outer margin of the uropodal exopod). In the tree on the left, the ancestral state in black indicates that the space between the distal spines of the telson is greater than one-third of the distal margin, the derived state in red indicates that it is equal or smaller. In the tree on the right, the ancestral state in black indicates that there is a single fixed tooth on the outer margin of the uropodal exopod, the derived state in red indicates that there are two or more fixed teeth, and ambiguous ancestral states are indicated in violet. These characters are useful in diagnosing species complexes within the Gambarelloides group that are well supported by the molecular data (Fig. 4-1).

Telson, distal margin space

Uropodal fixed teeth

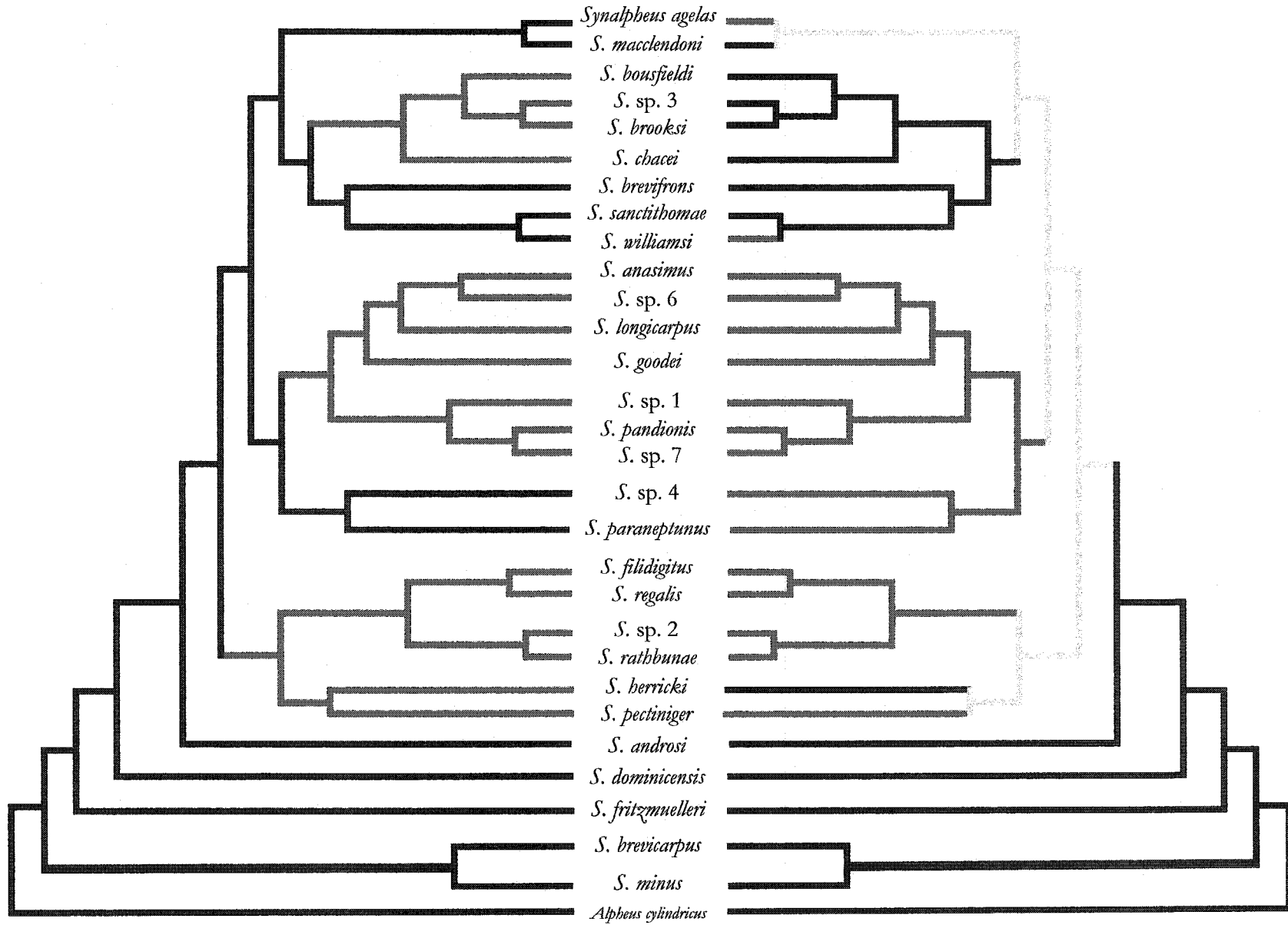
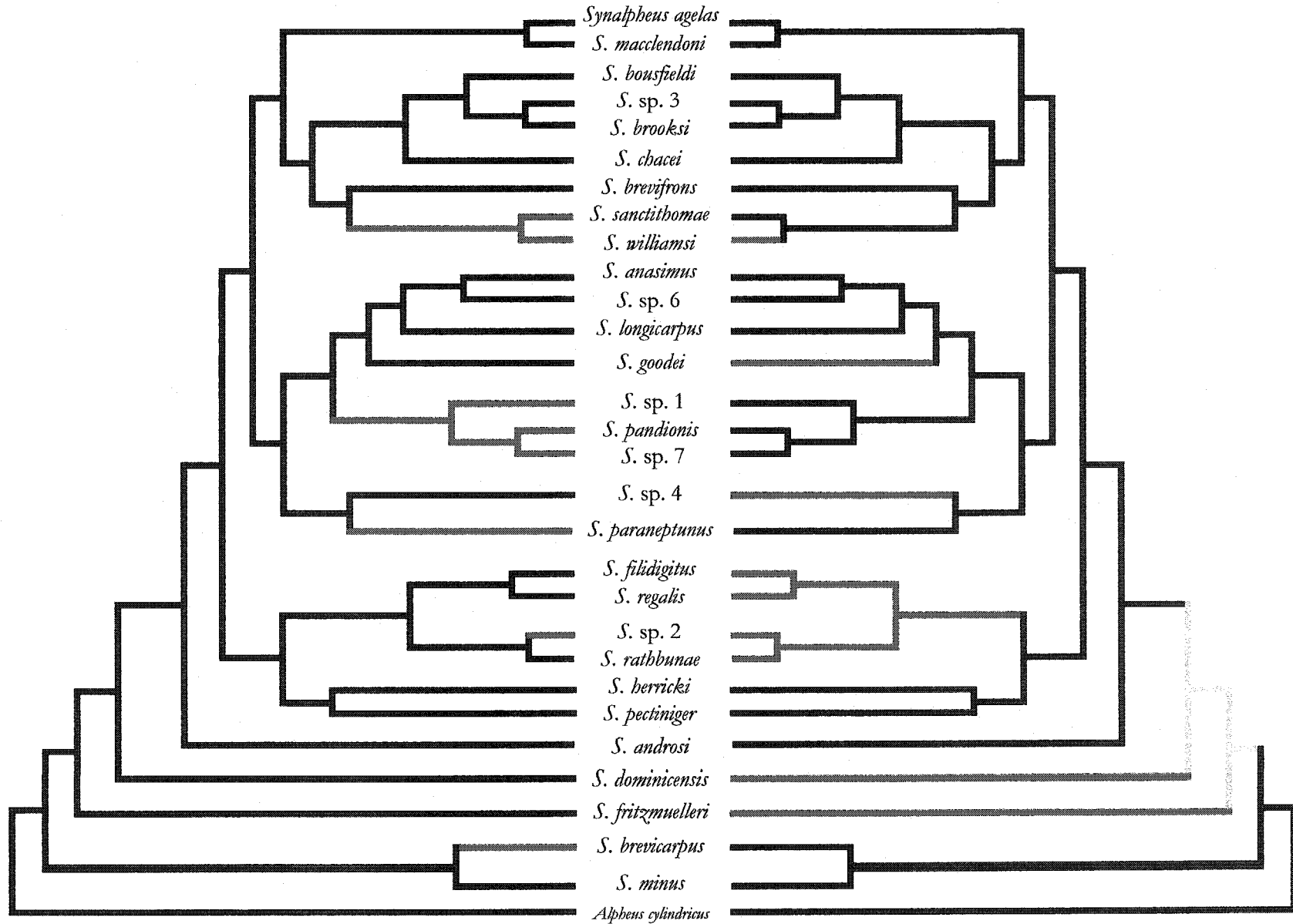


Figure 4-12. Evolutionary history of two traits showing parallelism; they provide a weak phylogenetic signal, but are taxonomically important and help to distinguish closely related species. Left: character 27, absence or presence of a basal protuberance on the outer face of the pollex of the major chela. Right: character 19, absence or presence of a spine on the dorsolateral corner of the basicerite. In both trees, the ancestral state in black indicates the lack of the structure and the derived state in red indicates its presence. The violet indicates ambiguous ancestral states.



Williamsian protuberance

Basicerite, dorsal spine



## CHAPTER FIVE

### General Conclusions

The description of a new species (*Synalpheus williamsi* Ríos and Duffy 1999, Chapter 1) and the discovery of seven undescribed species of *Synalpheus* Bate, 1888 in a relatively restricted area of the western Atlantic (Chapter 2 and 3) suggest that the diversity of this genus is considerably greater than previously thought. Within the family Alpheidae Rafinesque, 1815, *Synalpheus* is second only to *Alpheus* Fabricius, 1798 in species richness, but the diversity of the latter involves more dissimilar morphologies, for example in regard to the shape of both chelae of the first pair of pereopods, the shape of the front of the carapace, and the shape of the remaining legs. In contrast, in *Synalpheus* the morphology is remarkably uniform; the front of the carapace is always trispinose, the major chela is ovoid, and the posterior pereopods are usually indistinguishable among the species. Also, since many species of *Synalpheus* inhabit the internal canals of particular sponges, they can be found in great numbers (Beebe 1928). It might seem paradoxical that whenever abundant material of *Synalpheus* becomes available, as with the collection of several taxa studied here, species identification becomes problematic because the frequently pronounced intraspecific variability renders useless the subtle morphological differences generally used to define species. Nevertheless, availability of large collections also permits a statistical approach to diagnosing species (*e. g.*, Duffy 1996c), which we have been able to confirm with molecular data (Morrison, Ríos and Duffy, in press).

The establishment of different boundaries for intraspecific variability by different taxonomists previously has produced conflicting classifications in *Synalpheus*. For example, Dardeau (1984) accurately resurrected *S. pandionis* Coutière, 1909, from the synonymy of *S. longicarpus* (Herrick 1891) wherein Christoffersen (1979) had included it. Dardeau also

concluded with Chace (1972) that the blade on the scaphocerite of *S. pandionis* was a variable character. However, by constraining the limits of the variability of the blade, in combination with other characters, I have been able to distinguish at least three additional species (*Synalpheus* sp. 1, *S.* sp. 6, and *S.* sp. 7), which are supported by molecular data (Morrison, Ríos and Duffy, in press). Banner and Banner (1975) remarked that the intraspecific variation in *Synalpheus* can be truly confusing. Nevertheless, they concluded that “some rather small characteristics seemingly are constant”. This kind of character, autapomorphic until proven otherwise, is also present in some species of *Synalpheus* from the western Atlantic. Examples include the carpopal modification of the third pereopod in *S. androsi* Coutière, 1909, the tridentate fingers of the minor chela in *S. pectiniger* Coutière, 1907, the shallow frontal margin of the carapace in *S. brevisfrons* Chace, 1972 and the twisted major chela in *S. mcclendoni* Coutière, 1910. My final conclusion in this regard, is a sobering realization of the verdict of previous authors: the general morphology of the species of *Synalpheus* is remarkably uniform (Banner and Banner 1975), and the taxonomy is particularly complex not only because of the scarcity of taxonomic characters, but also because of a high intraspecific variability in many species, and frequent homoplasy. In a somewhat facetious statement, Coutière (1908) noticed that within the Gambarelloides group of species in particular, “unstable characters have regrouped like in a haphazard combination of letters”. Given the abundance, diversity, and variability of the genus it is not remarkable that the systematics of *Synalpheus* is still in flux. Despite this intraspecific variability, my careful study of new collections of Caribbean *Synalpheus*, supported by detailed information on ecology and distribution (*e. g.*, Duffy 1992, 1996c), tends to support the species concept of Coutière (1909). By erecting species and subspecies for relatively minor morphological variants, Coutière could

be considered a “splitter”, but I have concluded that such morphological variants are often, indeed, good species.

Probably the most important conclusion of the current phylogenetic analysis is the considerable support for the monophyly of the Gambarelloides group of species, erected by Coutière (1908, 1909), wherein most of the species in the western Atlantic are included.

My analysis of the morphological characters most commonly used in taxonomy of *Synalpheus* corroborates the impression from much previous research that phylogenetically informative morphological characters are few in the genus *Synalpheus*, and moreover suggests that these do not seem to be concentrated in any particular region of the body. In my analysis, only two characters define the Gambarelloides group of species. First, the setal brush on the dactyl of the minor chela was traditionally recognized as one of the synapomorphies of the group (Coutière 1908 and 1909), despite its incomplete reversal in *S. paraneptunus* Coutière, 1909. The second character, the coxal lamella on the third leg, had not been previously recorded. Two additional characters might also be diagnostic for the Gambarelloides group: the length of the ventrolateral spine of the basicerite compared to the stylocerite, as already mentioned by Coutière (1909), and the tooth under the first segment of the antennular peduncle. The multiple fixed teeth on the uropodal exopod is a remarkable apomorphy, unique to the genus *Synalpheus*. Despite its secondary loss in most of the species in the clade that includes *S. bousfieldi* Chace, 1972, and in three other species, the presence of multiple teeth on the uropod seems to be restricted to the Gambarelloides group and is found nowhere else within the family Alpheidae. Except in cases of polymorphism, in which the same species may have 1 or 2 teeth, this character is easy to score and consequently has been widely used as a diagnostic character at the species level in *Synalpheus*. The material examined for this study suggests that not only is the

number of teeth important, but also their arrangement in relation to the mobile and fixed spines on the uropodal exopod. For example, in *S. goodiei* Coutière, 1909 the submesial fixed tooth is wider than in *S. williamsi* and also, the mobile spine is much shorter. My careful study of the morphology of Caribbean *Synalpheus* (Chapter 4), together with supporting molecular analysis (Morrison, Ríos and Duffy in press) leads me to conclude that the Gambarelloides group of species is a well-defined, monophyletic taxon. Thus, as an initial step towards the full revision of the taxonomy of the genus *Synalpheus*, I formally recommend the recognition of the formal subgeneric status for the Gambarelloides group of species.

A significant motivation for this systematic study of *Synalpheus* was the interesting ecology of these shrimps and their potential value for comparative studies in ecology, evolution, and behavior. *Synalpheus* is an excellent subject for evolutionary biology studies because of the profusion of closely related species with distinct ecological preferences, and intraspecific grouping strategies that include not only the pair-forming typical of alpheids (Knowlton 1980), but also subsocial and eusocial aggregations (Duffy, Morrison, and Ríos 2000). Indeed, *Synalpheus* includes all three marine species wherein eusociality has been documented (Duffy 1996a, 1996b, 1998; Duffy and MacDonald 1999). The availability of a revised phylogeny of the *Synalpheus* from the western Atlantic (Morrison, Ríos and Duffy in press, Chapter 4) provides a valuable framework for the study of the evolution of this genus. Given the abundance and diversity of *Synalpheus* species throughout the tropical seas of the world, it seems incongruous that our knowledge of the biology of this evolutionarily puzzling taxon is not only restricted to a few species (Duffy 2003), but also that *Synalpheus* has such an obscure taxonomic status, lacking even a proper definition of the genus (*vide* Verrill 1922, Banner and Banner 1975, and Chace 1988). The research presented here should begin to remedy this situation by establishing

an improved practical taxonomy of western Atlantic *Synalpheus*, and a better understanding of their phylogenetic relationships which can set the stage for rigorous comparative studies of ecology and evolutionary history.

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